THE CLASSIFICATION AND NATURAL HISTORY OF *THEROPITHECUS (SIMOPITHECUS)* (ANDREWS, 1916), BABOONS OF THE AFRICAN PLIO-PLEISTOCENE

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By C. J. JOLLY

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I. INTRODUCTION

The remains of large cercopithecoid monkeys are not uncommon in African Pleistocene and late Pliocene deposits, and many have been referred to extinct genera. One of the most frequently mentioned of these is *Simopithecus*. A thesis developed in this paper is that *Simopithecus* can be regarded as a subgenus of *Theropithecus*, a genus with a single extant species (*T. gelada*) confined to the high plateau of Central Ethiopia.

The earliest finds of fossil *Theropithecus* (= *Simopithecus*) were made by Dr Felix Oswald in 1911 at the site now known as Kanjera, close to the southern shore of the Kavirondo Gulf. Additional material was reported from the same site by Dr L. S. B. Leakey (1943a). Subsequent palaeontological explorations have documented the presence of the genus at almost all East African sites of Plio-Pleistocene age from which a representative fauna has been obtained: Olorgesailie (Cole, 1954; Isaac, 1966a), Olduvai (Hopwood, 1934, 1936; Leakey and Whitworth, 1958), Kaiso (Hopwood, 1939; Bishop, 1968), Omo (Arambourg, 1947; Howell, 1969), Koobi Fora (R. E. F. Leakey, 1970), and Lothagam (Patterson, Behrensmeyer and Sill, 1970). Freedman (1957) and Singer (1962) recount the discovery of the genus in South Africa, where it is known at Swartkrans, Makapan and Hopefield. Recognition of the genus at Ternifine, Algeria (Arambourg, 1962) extends its distribution to the extreme north of the African continent (Fig. 1). On the other hand, *Papio*

Fig. 1. Known occurrences of *Theropithecus*. 1. Ternifine. 2. *T. gelada*, present distribution. 3. Omo. 4. East Rudolf sites. 5. Lothagam, Kanapoi, Ekora. 6. Kaiso. 7. Kanjera 8. Olorgesailie. 9. Olduvai. 10. Makapan. 11. Swartkrans. 12. Hopefield.

(*Simopithecus*) *serengetensis* Dietrich 1942 from Laetolil, Tanzania, is almost certainly a *Papio* or *Parapapio* (Freedman, 1957). Leakey (1956) mentions postcranial fragments from Broken Hill, Zambia, which might be *Simopithecus*. While this is a possibility, the specimens might equally be derived from a *Papio* or other large, ground-living monkey.

Most of the material described in the literature consists of skulls, teeth, and cranial and dental fragments, but postcranial remains have been described by Andrews (1916) and Singer (1962).

The object of this study is to re-examine the taxonomy of the whole group, its relationship to other Cercopithecidae and its place in the Pleistocene ecosystem.

Original material from each of the East African sites was examined. This consisted of specimens previously mentioned or described (Andrews, 1916; Hopwood, 1934, 1936, 1939; Leakey, 1943a; Arambourg, 1947; Leakey and Whitworth, 1958) together with an extensive collection of material from Kanjera, Olorgesailie and Olduvai which had not been previously described. Much of this new material was unregistered at the time of writing. However, the considerable body of material from Olduvai described subsequent to 1961 was not included in the study, nor was the recently discovered material from Koobi Fora (R. E. F. Leakey, 1970). Both the series are currently under study by Dr Maeve Leakey. The very rich body of cranial, dental and postcranial material collected by the Chicago Omo Research Expeditions during 1968 and 1969 (Howell, 1969) was also unavailable at the time that the study was written. Assessment of the South African material was based largely upon detailed published accounts (Freedman, 1957, 1960; Singer, 1962) supplemented by casts of some of the material most generously made available by Mr Eric Delson.

The fossil material was compared with cranial and postcranial specimens of recent monkeys in the collections of the British Museum (Natural History), the Unit of Primatology and Human Evolution, Royal Free Hospital, and the American Museum of Natural History. Because skull form in the Cercopithecoidea is profoundly modified by allomorphosis (Reeve and Huxley, 1945; Freedman, 1962a, b), skull characters were compared primarily with the largest living monkeys; *Papio, Mandrillus* and *Theropithecus gelada*. *Macaca* was represented by one of its largest species, *M. nemestrina*. Each of the living Cercopithecinae used for comparison was represented by a substantial series in the British Museum collection.

Postcranial material used for comparison is listed in Table 1. This series represents the full range from the most arboreal (*Cercocebus albigena*) to the most terrestrial (*Theropithecus gelada*) of the living Cercopithecinae. Interpretations of skeletal features were checked by muscular dissections of cercopithecine limbs, as listed in Table 2.

Cranial specimens were measured for the most part following Freedman (1957). Four dimensions were recorded for each molar and three for each premolar tooth. Three molar dimensions (anterior and posterior breadth, length), are as defined by Freedman (1957). The fourth (estimated unworn length) is similar to length, but with a subjective correction for ante-mortem wear which is considerable in *Simopithecus*. Dimensions quoted from authors other than Freedman (1957) and Singer

TABLE 1

Cercopithecine comparative skeletal material

	Male	Female	?Sex	Wild-shot	Captive	History unknown	Adult	Subadult	TOTAL
Theropithecus gelada	3	—	—	—	3	—	3	—	3
Mandrillus	7	4	—	6	4	1	9	2	11
Papio	13	6	1	18	1	—	13	6	19
Cercocebus	4	1	—	4	1	—	4	1	5
Macaca	5	6	4	8	4	3	11	4	15
Cercopithecus	6	3	2	6	—	5	9	2	11
									64

TABLE 2

Muscular Dissections

	Sex	Age	Origin	Limbs Dissected
Presbytis entellus	M	Adult	Zoo	Fore
Papio cynocephalus I	M	Juvenile	Laboratory	Fore and Hind
P. cynocephalus II	M	Juvenile	Laboratory	Fore
T. gelada	M	Adult	Zoo	Fore and Hind
Cercocebus atys	M	Subadult	Zoo	Fore and Hind
Mandrillus sphinx	M	Subadult	Zoo	Fore and Hind

(1962) are usually of length and (maximum) breadth only, and perhaps differ slightly from the dimensions standardised by these authors and followed here.

Owing to sexual size dimorphism, it is necessary to distinguish specimens according to sex before comparisons in terms of size and statistical analysis are undertaken. Although it can be assumed that the biggest teeth in a variable sample will be male and the smallest female, the wide overlap between the sexes in dental size makes it impossible to sex the majority of specimens on size alone. Dental and cranial specimens were therefore sexed on morphological criteria. Specimens were thus allocated to one of three categories: *Male*, *Female* and *Unsexed*. For the sake of consistency, those specimens from South Africa which were sexed by Freedman on the grounds of size alone are here allocated to the *unsexed* group.

Mean, range, and sample variance (s^2) were calculated for each dental dimension for series of reliably sexed specimens. As *unsexed* teeth outnumber the other two categories in all cases except P_3, the overall range for all specimens from each site is also quoted. Descriptions of dental anatomy employ the terminology developed by Eric Delson for use in his forthcoming survey of cercopithecoid dentitions, and illustrated in Figs 2 and 3.

Postcranial specimens were compared with the modern series with especial reference to those features which have been found (Jolly, 1967) to be good indicators of terrestrial or arboreal adaptation. Measurements of two kinds were taken on postcranial material; those for calculations of indices of terrestrial adaptation, and others from which the unbroken lengths of the bones, and hence the general body-size of the animal and its limb-proportions, might be estimated.

Dental measurements were made with a sliding calliper equipped with a dial vernier and accurate to 0·1 mm. Cranial and postcranial dimensions were taken with sliding or spreading craniometric callipers graduated in millimetres.

In order to avoid excessive repetition, comparisons with other genera will be made in the body of the description of specimens, although general discussion is reserved for later sections.

II. DESCRIPTION OF SITES AND MATERIAL

A. KANJERA

The site of Kanjera, formerly known as Homa Mountain, is situated close to the southern shore of the Kavirondo Gulf of Lake Victoria. The earliest *Simopithecus* remains were recovered from the area in 1911 by Dr Felix Oswald (Andrews, 1916); extensive further collections were made by Dr L. S. B. Leakey (Hopwood, 1936, Leakey, 1943a; Leakey and Whitworth, 1958).

Kent (1942) describes the deposits as consisting of water-laid beds of volcanic ash, tuffs, and clays, and attributes their formation to a pluvial period. As well as a typical Middle Pleistocene fauna, the deposits contained pebble-tools and Acheulian hand-axes.

As a whole, the specimens from Kanjera are the best-preserved of the East African series. All are highly mineralised, hard and heavy. Surface detail of both bones and teeth is very finely preserved, there is no crumbling of the surface, and no evident post-mortem distortion, even in specimens consisting of almost complete skulls or mandibles. A very few specimens show damage due to weathering after surface exposure. The minimum number of individuals represented by the material is probably ten: four adult or sub-adult males, five adult or sub-adult females, and a juvenile female. Both cranial and postcranial skeletons are well represented.

Skull

The crania of both sexes and the female mandible are represented by almost complete specimens, the male mandible by more fragmentary examples.

a. F 3668 (Plate 3a and 4a)

An almost complete male cranium (figured in Leakey, 1943a; Leakey and Whitworth, 1958).

Apart from some damage to the lateral walls of the orbits, to the skull-base and to the right parietal region, the skull is virtually intact. All the permanent dentition is present, apart from the incisors, which are represented by stumps or empty alveoli. The tip of the left canine, and the lower half of the right, are also absent. The molars show some post-mortem damage. The third molars are not fully in occlusion, the posterior cusp-pair of both lying above the occlusal plane. The second molars and the pre-molars show moderate wear. The first molars show heavy wear, the dentine exposure on the occlusal surface being continuous over the whole tooth, obliterating the enamel infolding between the main cusp-pairs and also between these and the anterior and posterior projections.

The premaxilla is relatively small, with less bulging of the anterior surface over the roots of the incisor series than is seen in *Papio*, *Mandrillus* or *Macaca*, but rather more than in *Theropithecus gelada*. The inferior margin of the nasal aperture is much more horizontal than in *Papio*, *Macaca* and *Mandrillus*, and less pointed. Between the medial incisor roots, on the anterior face of the premaxilla, is an anteriorly-running groove, less deep than that seen in *Papio*, but deeper than that of the gelada. The lateral and inferior margins of the piriform aperture, apart from the region of the groove, are slightly raised and thickened, as is seen in some individuals of *Papio*, *Mandrillus* and *Macaca*. In *Theropithecus gelada* the lateral margins of the nasal aperture are sharp and not raised, and a pair of small, but prominent, conical tubercles are invariably present on either side of the midline on the inferior border. Probably these tubercles (mentioned by Vram, 1923) are associated with the cartilaginous support of the peculiar, upstanding external nose. The anterior surface of the premaxilla resembles that of *Papio* and *Macaca* in the ratio of its height to its width, rather than that of *Theropithecus gelada* which is higher and narrower. *Theropithecus gelada* also differs from the other monkeys examined, including *Simopithecus*, in the strong convexity of the anterior surface of its premaxilla. The skull agrees with the gelada, and differs from the other genera, in the very limited projection of the premaxilla anterior to the canines. The shape of the part of the premaxillary-maxillary suture visible on the surface of the palate resembles that of *Theropithecus gelada* more closely than those of the other genera in shape. The nasal processes of the premaxilla form the lateral margins of the piriform aperture, and extend on either side of it about 2 mm; much as in the modern species apart from *T. gelada*. In the latter, the nasal processes are very narrow and lie almost entirely within the aperture; this applies especially to the superior half of each process, which is narrowed by an abrupt angulation of the premaxillary-maxillary suture towards the midline. This feature is seen in all specimens of *Theropithecus gelada* and was distinguishable in an infant with full milk dentition, the youngest individual available.

The nasals are, relative to the size of the muzzle, very narrow; more narrow, absolutely, than in individuals of the other genera in which the whole muzzle is much less broad. The nasals are not raised above the smooth curve of the muzzle at any point in their length, unlike those of *Mandrillus*, which are always strongly raised, and *Papio*, in which they are usually raised. Those of *Theropithecus gelada* and *Macaca* are not raised, and resemble the condition in F 3668. The general contour of the nasals, as viewed from the lateral aspect, resembles that of *Papio* and *Theropithecus gelada*, with a sharp ante-orbital drop. The concavity of the facial profile is rather less than is seen in *Theropithecus*, and resembles that of *Papio*.

The flanks of the muzzle slope evenly from the midline to the alveolar margin, and are without the fossae seen in *Papio*, *Theropithecus gelada* and *Mandrillus*. In the gelada a deep maxillary fossa is present; this is outlined inferiorly by the inflated alveolar region covering the roots of the premolar and molar series and the flange joining this margin with the root of the zygoma; posteriorly by the deeply excavated malars which project abruptly from the surface of the muzzle, and superiorly by the slight angulation marking the border between the flank and the dorsum of the muzzle and the bulging of the maxillary surface over the root of the canine. In *Papio* and *Mandrillus* the elements forming the fossa are similar, but the ridge between the dorsum and the flank is more expanded, especially in *Mandrillus*, and in

Mandrillus and the larger forms of *Papio* the infraorbital excavation of the malar is less developed. In *Macaca* all the elements defining the maxillary fossa are absent, apart from a very slight expansion of the surface over the root of the canine and of the cheek-teeth. In the Kanjera specimen, the shape of the maxillary flank resembles that of *Macaca*, all the eminences outlining the fossa in the other genera being absent, apart from a slight expansion over the tooth-roots. The root of the zygoma runs smoothly into the surface of the maxillary flank without any appreciable angulation, and quite without excavation of its anterior surface. Two infra-orbital foramina are present on either side, close to the zygomatico-maxillary suture.

The supraorbital torus is shaped much as in *Papio, Mandrillus* and *Theropithecus gelada* and is rather more prominent than in most individuals of *Macaca*. It runs more or less horizontally across the brow, with only a slight, rounded depression separating its two halves; thus it contrasts in shape with the strongly-arched ridges seen in *Gorgopithecus* (Freedman, 1957, plate XLVIII). A supra-orbital notch is present, as in *Papio, Theropithecus gelada, Macaca* and *Mandrillus*.

The temporal lines, situated on the frontal bone, unite in the region of the bregma. Posterior to their point of union, a sagittal crest extends as far as the inion. In spite of minor damage to the crest, it can be seen that its highest point was at, or only slightly anterior to, the inion.

The shape of the calvarium resembles that of *Theropithecus gelada*, having a narrower post-orbital constriction than is found in the other modern genera. The nuchal crest is high, showing greater development than in any specimen of the modern series. In the temporal fossa, a prominent crest, situated on the part of the posterior wall of the orbit formed by the zygomatic bone, runs for several centimetres roughly perpendicular to the occlusal plane. This probably represents the anterior margin of the M. temporalis; in the gelada the crest is well-developed, in *Papio* it is present but less well-developed, while in *Mandrillus* its position is marked only by a rather weak line.

The anterior surface of the zygoma, as has been mentioned, is not grooved, ridged or excavated. Its general shape and the course of the zygomatico-frontal suture are as in *Papio* and the gelada. The zygomatic arches are evenly convex, enclosing broad temporal fossae, and are about as massive as in male individuals of *Papio* of comparable size. A conspicuous, roughened groove on the inferior surface, extending

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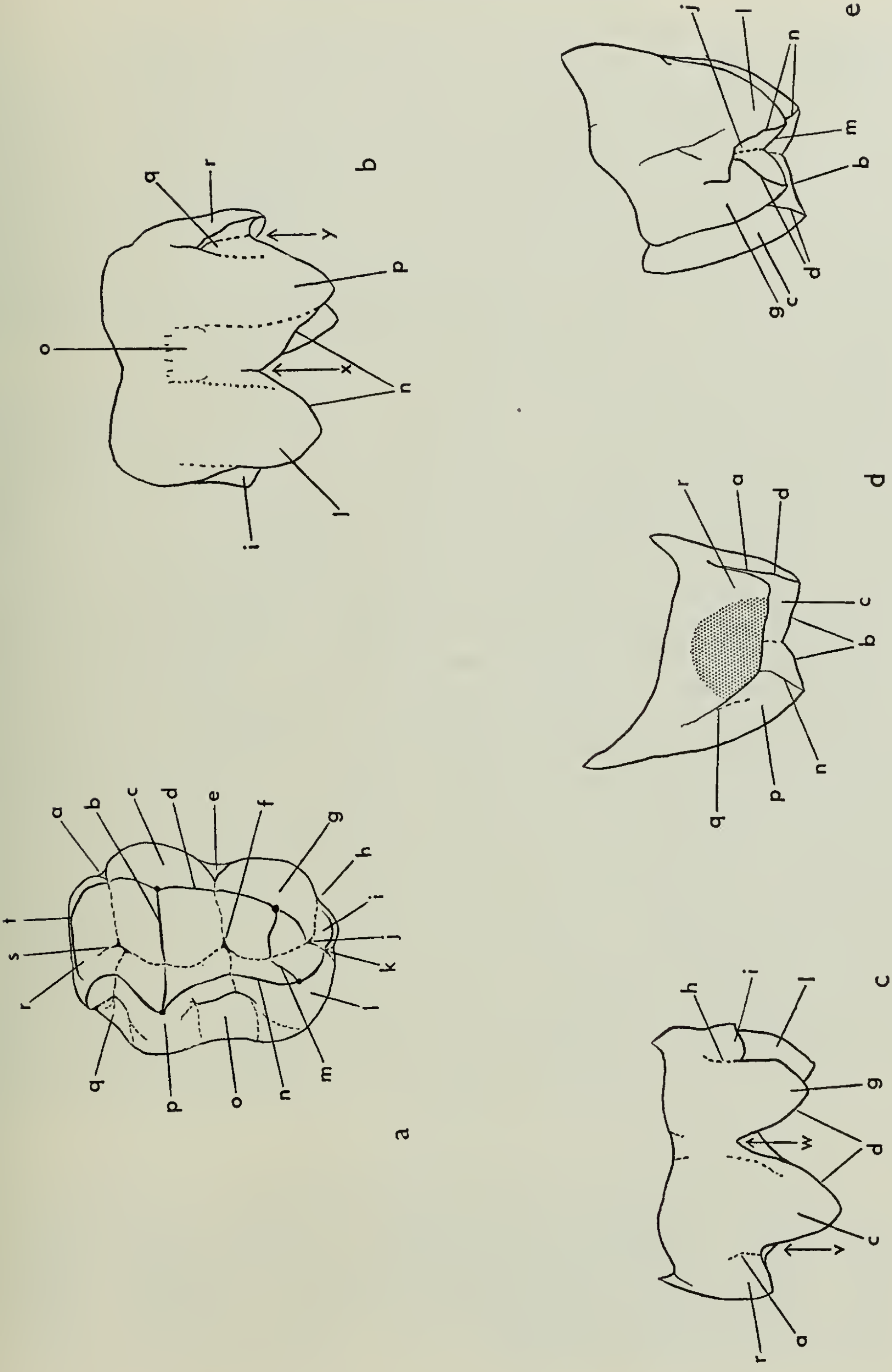
FIG. 2. Left, upper third molar of *T. gelada* to illustrate terms of dental anatomy used in this paper. A. Occlusal aspect. B. Lingual aspect. C. Buccal aspect. D. Mesial aspect. E. Distal aspect. a. Mesial buccal cleft. b. Protoloph. c. Paracone. d. Buccal margin. e. Median buccal cleft. f. Trigon basin. g. Metacone. h. Distal buccal cleft. i. Distal shelf. j. Distal fovea. k. Distal lingual cleft. l. Hypocone. m. Hypoloph. n. Lingual margin. o. Median lingual cleft. p. Protocone. q. Mesial lingual cleft. r. Mesial shelf. s. Mesial fovea t. Mesial margin. u. Distal buccal notch. v. Mesial buccal notch. w. Median buccal notch. x. Median lingual notch. y. Mesial lingual notch. Stippled area: contact facet for M^2. Grooves are represented by interrupted lines; crests and ridges by solid lines.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as far anteriorly as the angulation of the malar, represents the origin of the M. massetericus. Such a groove is present in the modern genera examined.

Viewed from the inferior aspect, the palate is more or less rectangular in outline, with the two stout canines standing at the anterior corners. There is, however, a distinct increase in the external breadth of the palate across the second molars, the tooth-row converging slightly both anterior and posterior to this. The two rather small anterior palatine foramina are situated in much the same position, relative to the tooth row, as in *Papio* and the gelada. The posterior palatine foramina are situated opposite the posterior cusps of the third molars; rather more anteriorly than in male specimens of *Papio* of comparable size and age; the feature is however a variable one. The anterior end of the vomer is preserved; this is thicker and stronger than the same element in any of the modern specimens.

Much of the base of the skull, including the part of the basi-occipital surrounding the foramen magnum, and most of both petrous temporal bones are missing; the external auditory meatus are however preserved, and it can be seen that they face rather more directly laterally, and less posteriorly and upwards than in *Papio*, *Theropithecus gelada* and *Mandrillus*. *Macaca* is rather closer to the fossil in this respect, having less posterior inclination than in the other recent genera, but in this genus too the meatus faces somewhat posteriorly. The mastoid area as a whole is somewhat raised above the level of the basi-occipital, as in most individuals of *Theropithecus gelada* and some *Papio* and *Mandrillus*. A rather prominent, conical true mastoid process is also present; this feature was found to be highly variable in the comparative series, both in degree of development and in distinctness from the surrounding surface. A process resembling that of this specimen of *Simopithecus* was found in at least one specimen of *Papio*, and in several *Macaca nemestrina*. None of the series of geladas or *Mandrillus* was found to have as well developed a mastoid process. The area of the mandibular articulation differs from that seen in *Papio* and *Mandrillus* in that it consists of two distinct surfaces, with an angulation between them. The larger and more lateral of these is transversely flat, but anteroposteriorly convex; the smaller, lying medial to the last, is convex in both dimensions and faces slightly laterally. In *Papio* and *Mandrillus* the articular surface is transversely evenly concave, but agrees with that of F 3668 in its anteroposterior convexity. In *Theropithecus gelada*, the condition resembles that seen in F 3668 but the smaller, medial face is less distinct, and less lateral facing. Both post-glenoid processes are absent, but the position of each can be distinguished. The lateral end of the external auditory meatus lies in contact with the post-glenoid process anter-

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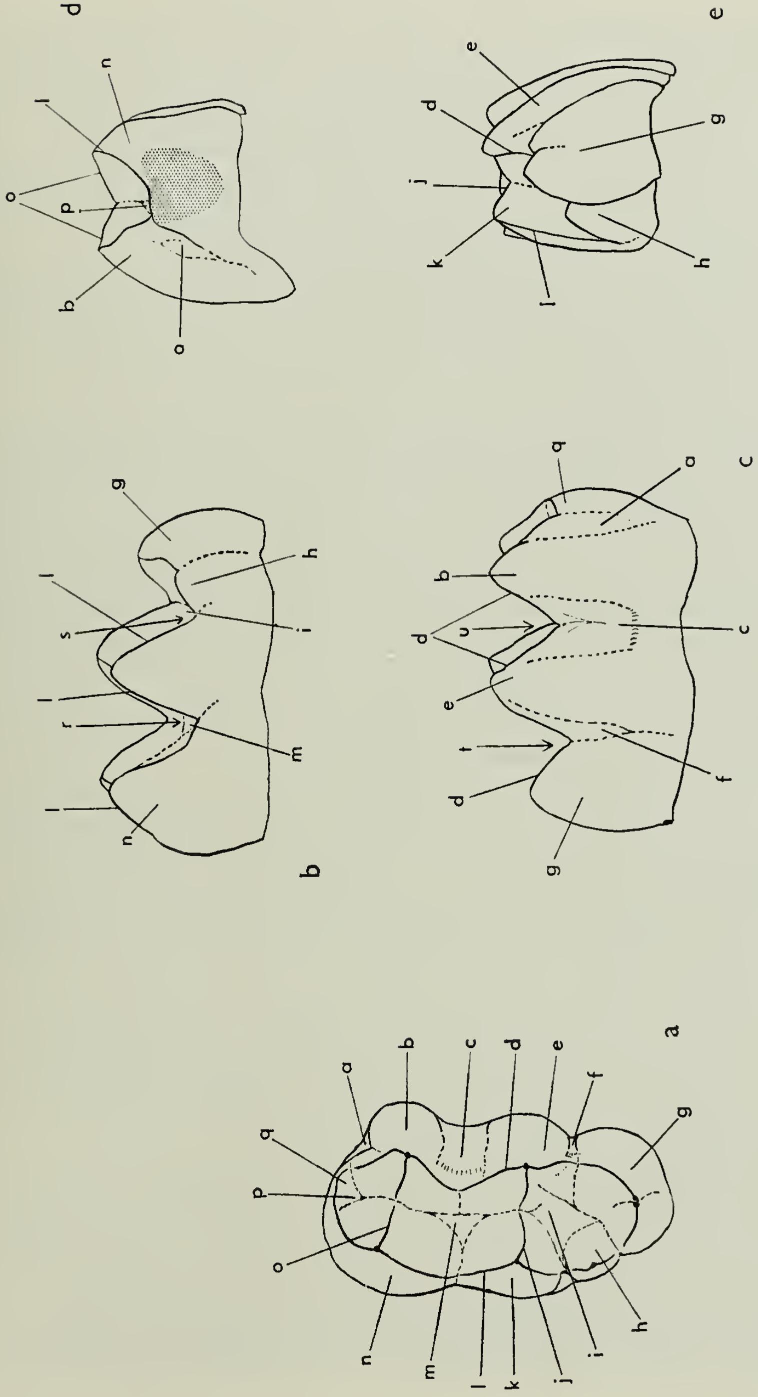
Fig. 3. Right, lower third molar of *T. gelada*. A. Occlusal aspect. B. Lingual aspect. C. Buccal aspect. D. Mesial aspect. E. Distal aspect. a. Mesial buccal cleft. b. Protocone. c. Median buccal cleft. d. Buccal margin. e. Hypoconid. f. Distal buccal cleft. g. Hypoconulid. h. Tuberculum sextum. i. Distal fovea. j. Hypolophid. k. Entoconid. l. Lingual margin. m. Talonid basin. n. Metaconid. o. Protolophid. p. Mesial fovea. q. Mesial shelf. r. Median lingual notch. s, Distal lingual notch. t. Distal buccal notch. u. Median buccal notch.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iorly, and the mastoid process posteriorly. This condition is not found in adults of *Papio*, *Mandrillus* or *Theropithecus gelada*, a distinct gap being invariably present between the meatus and the post-glenoid process. Some individuals of *Macaca* and *Cercocebus* have the meatus articulating with the post-glenoid process, and the condition seems to be regular in *Cercopithecus*, *Erythrocebus* and *Colobus.*

The basi-sphenoid is short and broad, as in *Theropithecus gelada.* Most of the basi-occipital is absent, but the sphenoid surface of the basal suture is intact, showing the latter to have been open at the time of death.

The pterygoid fossa is rather deep; it is divided into two by a ridge, beginning on the lateral wall of the medial pterygoid plate, running anterolaterally on to the medial wall of the lateral pterygoid plate, and ending in a tubercle on the free margin of the latter about a centimetre posterior to the palatine-maxillary suture.

b. M 14936 (Plate 5)

Reconstructed female skull (figured in Leakey and Whitworth, 1958).

Apart from the palatine and pterygoid region, which is mainly absent, and a small amount of damage to the lateral wall of the orbit and to the zygoma, the left half of the specimen is virtually complete. The missing regions have been in part restored in plaster of paris. The basal region, including the margins of the foramen magnum, is preserved, and the frontal is complete. On the right side, the upper part of the calvaria and parts of the region of the temporal fossa, including fragments of both the sphenoid and the temporal, are preserved, together with the post-glenoid process and the part of the temporal forming the root of the zygomatic arch. The more anterior parts of the right maxilla are also preserved. The rest of the right facial region, calvaria and zygoma have been reconstructed in symmetry with the left side, incorporating the fragments described.

On the left side, the molars and fourth premolar are preserved, together with the canine. The third premolar is represented by roots broken short at alveolar level. On the right side the molars and fourth premolar are again present, the former all showing some post-mortem damage. The canine is represented by a broken stump. None of the incisors is preserved, all being represented by roots or by empty alveoli. The individual evidently died shortly after reaching dental maturity; the third molars are fully erupted and in occlusion, with slight wear on all cusps. M^2 and P^4 show moderate, and M^1 extreme, attrition.

The premaxilla is somewhat damaged, the region of the inferior border of the nasal aperture being most affected. It can be seen that it was of the same general shape as in the male specimen; relatively rather small, scarcely projecting anteriorly beyond the canines; the lateral margins of the piriform aperture are somewhat raised and thickened, again as in the male specimen.

The muzzle slopes evenly from the midline to the alveolar margin, with only the slightest angulation between the dorsum and the flanks. The very slight maxillary depression is formed by the low inflation over the canine root and the buccal roots of M^1, both of the latter being exposed. The shape of the zygomatic root, sweeping into the surface of the flank of the muzzle without a distinct angulation, resembles the condition seen in the male specimen. The zygomatic arch itself is stout and strongly bowed. The areas of origin of the M. massetericus are deeply grooved and ridged, especially at malar angle, where, as in the male specimen, a distinct tubercle is present. The mandibular articular surface is antero-posteriorly narrow and convex. and evenly concave transversely; thus it resembles the normal shape in the modern Cercopithecinae more than does F 3668. The post-glenoid process is both longer and stouter than in any of the modern series. The skull-base is relatively broad. The external auditory meatus is directed as in the male specimen, more directly laterally than in the modern genera. The hypoglossal, jugular and carotid foramina are visible on the right side. All lie very close together, and the hypoglossal foramen is scarcely visible from directly below, being concealed by the occipital condyle. The posteromedial wall of the foramen ovale is absent; the antero-lateral wall is formed of the sphenoid. The left mastoid region is preserved; a prominent, conical mastoid process is present. As in the male specimen, the external auditory meatus is in contact with both the mastoid process and the post-glenoid process.

The supra-orbital ridge resembles that of the male specimen. The superior and inferior temporal lines of each side are close together, forming a raised ridge. The superior lines meet exactly at the bregma; the inferior lines come close to meeting in this region, but then run almost parallel for most of the length of the sagittal suture, finally meeting about 4 cm anterior to the inion. Posterior to their point of meeting a low sagittal crest is formed. The nuchal crest is present as a flange, lower than that of the male, but higher than in females of the modern genera, which reaches its maximum development lateral to the inion. No prominent external occipital protuberance is present.

c. A fragmentary female skull (unregistered) (described by Leakey, 1943a), reconstructed in plaster. The parts preserved include the frontal, a fragment of the cranial vault, mainly of the right side but including the region of the inion; the right zygomatic and most of the maxilla of the same side, as far anteriorly as the alveolus of P^3, part of the left zygomatic, including the malar angle; and the part of the left zygomatic arch formed by the temporal bone. The complete dentition is present, $M^3 - P^3$ of the right side in their alveoli, the rest of the teeth set in plaster. The third molars were about to come fully into occlusion at the time of death, with noticeable wear only on the extreme tip of the antero-buccal cusp. The specimen was therefore slightly younger at the time of death than the male described above. The maxillo-zygomatic and zygomatico-temporal sutures are more obviously open and loosely-knit than those of the previously-described female specimen.

The shape of the facial region is very much as described for the previous female specimen. The reconstruction of the skull probably errs in making the anterior border of the premaxilla too broad and flat, underestimating the convergence of the anterior ends of the tooth-rows. Three infra-orbital foramina are present in the preserved maxilla, immediately adjoining the maxillary-zygomatic suture. A zygomatico-facial foramen is also present, at the level of the inferior border of the orbit. The superior and inferior temporal lines are similar to those of the last specimen. They are prominent in the region of the temporal fossa, sweeping together and almost meeting at the bregma. The superior temporal lines meet slightly posterior to the bregma (this region is somewhat damaged); the inferior temporal lines do not meet, but run parallel, about 5 mm apart, and then diverge on approaching the nuchal line. Both lines are visible in the region of the inion, meeting the nuchal crest about 12 mm apart.

d. Unregistered

The right glenoid region of a skull, with a complete post-glenoid process (figured in Leakey and Whitworth, 1958.)

The post-glenoid process is extremely stout and long. The morphology of the rest of the fragment resembles that of F 3668; it is slightly larger than the corresponding reigon of the latter, and therefore probably represents a fully adult individual.

e. M 11537 (Plate 7c and d)

An almost complete muzzle region, with both maxillae, and part of the zygomatic bones of both sides present, rather more on the left than on the right side. Also a very small part of the left premaxilla, forming the inferior lateral margin of the piriform aperture. On the left side, the cheek-tooth row is complete; on the right, all the molars and premolars and the canine are present. In the premaxillary fragment, the roots of the left incisors are visible. All cheek-teeth, apart from M^3 and P^3, show rather extreme wear. From the small size of the canine, the specimen is obviously female.

The shape of the flanks of the muzzle agrees exactly with the condition seen in the female specimens described above; the very slight hollowing of the maxillary surface is due entirely to a small swelling of its wall over the roots of the molars. The bone covering the buccal roots of the molars is extremely thin, and some of the latter are in part exposed. The shape and orientation of the zygoma is exactly as in the other female specimens, without fossae or distinct angulation. With the occlusal plane horizontal, the most inferior point of the zygomatic root lies above the anterior cusps of the third molar.

f. M 18720 (Plates 6c and 7a and b)

A complete premaxilla, with adjoining parts of the left and right maxillae, to the level of P^4. Both left, and the lateral right incisors are present. All premolars are present, and show slight wear. The small size of the canines shows the specimen to be female.

A deep medial groove is present between the incisors; apart from this region, the premaxillary part of the inferior and lateral margins of the piriform aperature is slightly raised, confirming the condition seen in the more complete male and female skulls described above. Almost certainly from the same individual as:

g. M 11538 (Plate 7a and b)

The posterior part of a maxilla, with the molars preserved. The first and second molars show slight to moderate wear; the third is fully erupted and in occlusion, but shows very slight wear on the anterior pair of cusps only. The maxillary surface, as in the other specimens, is smooth, without a fossa. The roots of the molars are covered by only a thin layer of bone; both the buccal roots of M^1, and the anterior buccal root of M^2 are exposed. Four infra-orbital foramina are present, all situated on the maxillary-zygomatic suture. Three are situated close together in a single pit in the maxillary surface. The posterior palatine foramen is visible, opposite to the posterior cusps of the third molars.

h. M 18767

Part of a cranial vault, mainly of the right side; includes the posterior part of the parietal, with the inion and sagittal crest preserved, together with a small part of the temporal.

The structure of the sagittal crest resembles that seen in the more complete specimens.

Registered under the same number is a fragment of the frontal from the right supra-orbital region, including the superior surface of the orbit. The superior and inferior temporal lines are so close together as to give the impression of a single, raised line. Judging from the close approach of the line to the midline of the vault, it probably met its fellow anterior to the bregma.

i. M 18765 (Plate 4b)

Frontal fragment, together with the extreme upper parts of the nasals. The supra-orbital tori are mostly absent, but the glabella region preserved. The temporal lines are prominent, converging to meet well anterior to the bregma. The two lines are asymmetrical, that of the right reaching rather higher on to the cranial vault than that of the left.

j. M 18764 (Plate 8a and b)

Part of the superior surface of the cranial vault, together with a small part of the nuchal surface. The temporal lines converge to a point anterior to the bregma, posterior to which a rather high sagittal crest is present. Although the free margin of the crest is somewhat damaged, it can be seen that its highest point was probably anterior to the inion.

k. M 18766

Two fragmentary frontal bones. Both show a pattern of development of the temporal lines similar to the specimens described.

l. F 3394 (Plate 4c)

An almost complete frontal, only slightly damaged by surface erosion. The shape of the supra-orbital region and the pattern of the temporal lines agrees with the specimens described. The temporal lines converge to meet almost exactly at the bregma.

m. M 11539 (Plates 9b and 10a)

An almost complete female mandible (Type of *S. oswaldi* Andrews; figured by Andrews 1916, Leakey and Whitworth, 1958).

The specimen is complete apart from the gonial region of either side and the right coronoid process. On the left side the molar and premolars are all present; on the right, the molars are preserved, but the premolars are broken off at alveolar level. The incisors are represented by broken stumps or roots.

The third molar is fully erupted, in occlusion and shows light wear, the central 'bridge' between the cusp-pairs being unopen. The remaining cheek-teeth show moderate or heavy wear.

The corpus is more robust than in females of *Papio* and *Theropithecus gelada* and there is only the slightest trace of a mandibular fossa, immediately posterior to the canine and below the premolars. The anterior surface is not grooved and ridged by the roots of the incisors, as in *Papio*. Four mental foramina are present, situated below P_4 and the anterior cusps of M_1. The internal surface of the symphyseal region may be described in terms of an upper and a lower shelf, connecting the two halves of the mandible, and a pit on the internal aspect of the symphysis which separates the two shelves. The superior shelf extends backwards to the level of the posterior margin of the fourth premolar, further than in females of *Papio* (in which it extends approximately to the level of the posterior margin of the third premolar) and *Theropithecus gelada*, in which it reaches approximately the midpoint of P_4. Its superior surface is much less excavated than in any modern cercopithecoid genus. With the occlusal plane horizontal, the inferior ('simian') shelf extends posteriorly as far as the rear of the first molar, again more extensively than the corresponding shelf in *Papio* and *Theropithecus gelada*. The gonial region is mainly absent, but it is apparent that the bone thins rather abruptly posterior to the position of the roots of the molars, and that the gonial angles themselves were inverted, as in the modern forms.

The anterior margin of the ascending ramus bears, near its base, a prominent tubercle, which represents the area of attachment of the tendinous part of the insertion of M. temporalis. The coronoid process is strong. Immediately below it, on the lateral surface, is a conical tubercle, pierced by a foramen; this is presumably pathological in origin, since it is absent in all individuals of the comparative series, and in the other *Simopithecus* specimens in which the region is preserved. On the internal aspect, a raised crest runs upwards to the base of the coronoid process; this ridge, which is present in *Theropithecus gelada*, but not in *Papio* or *Macaca*, probably marks the limit of the extent of the insertion of M. temporalis on the internal aspect.

The articular surface of the condyle is rather flat, demarcated by a lip, and shows the lack of lateral expansion mentioned by Leakey and Whitworth as characteristic of the genus. On the posterior surface, immediately below the articular surface, is a distinct depression. As preserved, the angulation of corpus to ramus is somewhat less steep than in *Theropithecus gelada* though steeper than in *Papio* of comparable size. The angular region is somewhat damaged, however, and may be distorted in reconstruction. In any case, the ramus of the mandible belonging to M 14936 must have been both higher and more vertical.

n. F 3398 (Plates 9c and 10b)

A juvenile female mandible, complete apart from the coronoid processes, and the posterior margin and condyle of the right ascending ramus (described by Leakey, 1943a).

The dentition is almost complete. The incisors and canines are present and well-preserved. P_3 is fully erupted, and its tip is slightly worn. The tip of P_4 is just emerging from the alveolus, and the left is still covered by the milk-molar. M_1 is fully erupted, and shows wear on all its cusps, but the waist of dentine between the anterior and posterior cusp-pairs is not open. M_2 has reached a stage of eruption where the anterior cusps are in the occlusal plane, but show no wear; the posterior cusps are still below this level. M_3 had not started to emerge from the alveolus at the time of death, but the germ of the crown of the left M_3 has been dissected from its crypt.

As might be expected in a juvenile individual, the mandibular corpus is lower and more lightly-built than that of the adult female specimen, M 11539. The inferior surface of the symphysis is flat. The two shelves on the internal aspect of the symphysis are less backwardly-extended relative to the dentition than in the adult individual; the superior shelf extends back as far as the posterior cusps of the third premolar, the inferior shelf to the level of the posterior margin of the fourth premolar. The very shallow excavation of the superior surface of the upper shelf, however, resembles the adult condition. The external surface of the corpus is without a fossa. From the lateral aspect, the inferior margin of the corpus is slightly expanded in the region of the insertion of the M. masseter. The bone becomes thin in the gonial region, which is slightly inverted, and bears three tubercles on its internal surface. The lipping of the articular surface of the condyles, and the depression on the posterior surface, resemble the condition described in the adult, but the internal expansion of the articular surface is less pronounced.

o. M 18770

A mandibular fragment, consisting of the posterior part of the corpus, without the gonial region. The roots of the third molar, a worn and broken second molar, and a fragment of the posterior root of the first molar are present. This fragment confirms the robusticity of the corpus, and the thinning of the bone towards the gonial region, observed in the previous specimens.

p. M 11541 (Plates 9a and 10c)

A fragment of a left, adult mandibular corpus, with P_4–M_3 present. The first molar is broken; the second shows moderate to heavy, and the third moderate attrition. P_4 is moderately worn.

The features of this specimen resemble those of M 11539, except that the inferior margin below M_1 and P_4 is slightly flared laterally, so that a shallow mandibular fossa was probably present.

q. M 19011 (Plate 8c and d)

A fragment of a right mandibular corpus, with P_3–M_2. The small size of the P_3 indicates a female individual. P_3 is newly erupted, with only very slight wear on the tips of the cusps. P_4 is moderately worn, M_1 shows heavy, and M_2 moderate to heavy wear. The inferior margin and the inferior half of the corpus is absent, but the outline of the superior symphyseal shelf is visible. This extends posteriorly as far as the posterior part of P_4, as in M 11539.

r. M 19012

The left ascending ramus of a mandible, complete except for the margin of the notch and the coronoid process. No teeth are present, but the impression of the posterior root of M_3 can be seen on the anterior, broken, surface of the fragment. The position of this shows that the individual was probably adult at the time of death. The details of the condyle resemble those described in M 11539, with lipping and the posterior fossa, but again the internal expansion of the articular surface, though more pronounced than in the modern forms, is less great than in M 11539. The bone of the gonial region is thin, with very slight inferior expansion of the area of insertion of the M. masseter. The margin is somewhat inverted, and three promiment tubercles, representing the area of insertion of the M. pterygoideus internus, are present. The area of temporal insertion is as described for M 11539, but the fossa is slightly deeper.

s. Unregistered

A fragment of the symphyseal region of a male individual, including the inferior surface, part of the internal surface, and the posterior surface of the alveoli of the canines.

The inferior surface of the symphysis is flat. The alveoli of the canine roots are close together at their inferior ends, and then diverge; the space between them for the incisors is relatively narrower than in any of the modern forms. Three mental foramina are present, near the inferior margin of the corpus.

t. Unregistered

An isolated right mandibular condyle (figured in Leakey and Whitworth, 1958). The morphology of this specimen, which from its size is almost certainly male, resembles that of the specimens described above. The internal extent of the articular surface resembles the condition seen in M 19012 and F 3398.

Teeth

The characteristic features of the molars and premolars of *Simopithecus* have been described in some detail by Leakey and Whitworth (1958), Freedman (1957) and Singer (1962), and are best appreciated by reference to the illustrations (Figs. 2, 3; Plates 6–10). The molars of both sexes, when compared to those of large Cercopithecinae of other genera appear large, and, when unworn, distinctly hypsodont, with strong contrast between the high, columnar cusps and the deep fovae.

One of the more distinctive features is commonly described (Leakey and Whitworth, 1958) as a high, longitudinal ridge connecting hypoconid and protoconid in the lower molar, and protocone and hypocone in the upper. This feature is in fact due to modifications in structures which are present in all cercopithecine molars, rather than the appearance of a new structure. Upper molars are in this respect mirror images of lower which are described here.

First, the talonid basin itself is deep, with a comparatively horizontal floor and vertical buccal face. This buccal face forms the lingual wall of the 'buccal longitudinal ridge'. On the buccal side, the median buccal cleft is deep, and is also bounded by comparatively vertical faces. Its lingual face forms the buccal wall of the longitudinal ridge. The supposedly distinctive appearance of the worn *Theropithecus* (*Simopithecus*) molar occurs when wear has reached the stage at which the occlusal surface is at the level of the base of the median buccal notch. At this stage of wear, a dentine 'bridge' opens between the lakes of dentine representing the truncated bases of the protoconid, metaconid and protolophid (mesially) and the hypoconid, entoconid and hypolophid (distally). The single dentine lake now has an asymmetrical hour-glass form, with the central bridge running along the crest of the buccal margin. All cercopithecine molars will pass through this stage of wear, and will show the hour-glass pattern of dentine exposure with a median longitudinal ridge until the floors of the talonid basin and the median buccal cleft lose their enamel. Since the cusps are high, and the floors of the foveae relatively low, in *Simopithecus* this stage is more prolonged than in other Cercopithecinae.

The lingual margin of the lower molars is no higher than in other Cercopithecinae, so that the flat-floored talonid basin appears to be broadly open lingually. It is, however, defined lingually by a ridge upon which are usually one or more cuspules. A similar condition is characteristic of the trigon basin in the upper molars, which is distinctively open bucally and bounded by the comparatively low buccal margin. The mesial fovea is also deep, and extends mesio-lingually as a deep fissure partially encircling the base of the metaconid, separating the latter cusp from the mesial shelf, which is thus demarcated as a prominent almost loph-like ridge connected to the protoconid. The mesial end of the tooth is further demarcated by the mesial buccal groove, which, while present in other large Cercopithecinae, is deeper and wider in *Simopithecus*. With wear, dentine exposure spreads mesio-lingually along the ridge from the protoconid, as in other Cercopithecinae and also, distinctively, mesio-*buccally* along the crest of the ridge defined by the deep mesio-buccal grove. At this stage of wear, therefore, the *Simopithecus* tooth presents a distinctive appearance, from the occlusal aspect, with a subsidiary area of exposed dentine in the shape of a symmetrical letter T connected to the protoconid- metaconid-protolophid dentine lake by its stem.

In the upper molars, precisely complementary peculiarities are seen in the mesial end of the tooth. The mesial fovea is deep, and the mesial lingual groove, which is variably but weakly developed in other large Cercopithecinae, is deep and extensive, so that the distinctive T-shape appears with wear.

Similar modifications are seen at the distal end of the tooth. In lower M_1–M_2 the floor of the distal fovea is low and broad, and the fovea itself opens lingually through a deep distal lingual notch. On the buccal side the distal buccal groove is deep. In the upper molars, the distal fovea opens through a deep distal buccal notch, and the distal lingual groove, which is weak or absent in large Cercopithecinae of other genera is deep.

Mesially, the lower M_3 is similar to M_1 and M_2. However, as in all Cercopithecinae apart from the tribe Cercopithecini, it bears a hypoconulid on the margin of its distal shelf, in line with, or slightly lingual to, the line connecting protoconid and hypoconid. As in M_1 and M_2, the distal fovea is deep, and its lingual margin is low. No examples were found with a tuberculum sextum (Swindler et al., 1967) approaching the hypoconulid in size. However, the flat, low floor of the distal fovea is crossed by grooves which define low cusplets along its raised margin. The distal buccal groove is again relatively broad and deep, and, like the median groove, its steep lingual wall, and that on the buccal side of the distal fovea define, between them, a continuation of the 'buccal longitudinal ridge' from hypoconid to hyperconulid.

P_3 is of the usual form for Cercopithecoidea; it is a unicuspid tooth whose predominant feature is the long, plane, sectorial face sweeping mesio-buccally from the summit of the protocone. The development of this face is clearly sexually dimorphic, the male being much the larger. However, compared to similarly sized males of *Papio*, and still more *Mandrillus*, the sectorial face is short relative to the length and breadth of the talonid. The talonid basin, on the other hand, is large. In females, the deviation from the condition in other large Cercopithecinae is much less noticeable.

P^3 and P^4 are very similar in structure, although P^4 is distinguished by its more symmetrical outline, its lingual margin being more nearly equal to the buccal than in P^3. They differ from their homologues in other large Cercopithecinae principally in having rather deeper basins, and by exhibiting two vertical grooves on the lingual surface, one mesial, the other distal to the protocone. On the buccal side, P^4, especially, hows traces of similar grooves defining a column topped by the paracone. The canines show considerable sexual dimorphism. Female upper and lower canines are not dissimilar from the equivalent teeth in other large Cercopithecinae although they appear small by comparison with the large cheek teeth. The male upper canines, however, even when relatively unworn as in F 3668, are much less high crowned than those of male *Papio*, *Mandrillus* and *Theropithecus gelada*, both in comparison with the size of the animal, and with the robusticity of the canine itself. The flange which runs from the distal buccal corner of the tooth-crown to its tip, and which, when honed against the sectorial face of P_3, bears a sharp cutting edge, is less distinct that in *Papio*, and much less than in *Mandrillus*. The male lower canine is represented by the isolated, worn specimen M 18729. Its unworn height cannot be reconstructed.

The male upper incisors are not known, but to judge from the size and orientation of their roots in F 3668, they must have been relatively small and vertically-placed.

TABLE 3

Cranial Dimensions in *Theropithecus*

	No. in descriptive list	Sex	Greatest Length	Prosthion-Glabella	Inion-Glabella	Post-orbital Constriction	Basion-Prosthion	Basion-Bregma	Temporal Breadth	Mastoid Breadth	Inion-Basion	Muzzle breadth at M^2	Bizygomatic Breadth
T. gelada series													
Mean ±	—	M	172·8	94·5	105·0	41·9	126·2	67·4	72·3	83·1	53·2	48·1	110·4
Variance			±	±	±	±	±	±	±	±	±	±	±
(N=13)			42·5	48·4	11·2	4·1	32·5	3·8	7·5	4·5	4·5	6·4	9·8
T. gelada,													
Mean of 2		F	158·5	81·0	97·5	43·0	111·5	62·0	68·5	78·5	50·0	45·0	—
Kanjera													
F 3668	a	M	207·0	114·0	125·5	47·0	—	—	83·0	100·0	—	60·0	134·0
M 14936	b	F	172·0	88·0	118·0	50·0	114·0	70·5	79·0	87·0	54·0	56·0	116·0
M 11537	e	F	—	—	—	—	—	—	—	—	—	53·0	—
Olduvai													
Bk II 1957	d	F?	—	—	128·0	56·0	—	76·0	85·0	106·5	62·5	—	—
Swartkrans													
SK 561*	—	F	—	(90)	—	47·0	—	—	—	—	—	—	—
Hopefield													
8400**	—	?	—	—	121·5	50·0	—	—	—	94+	—	—	—

* from Freedman, 1957.
** from Singer, 1962.
\+ 'Maximum bi-auricular breadth', which is probably close to mastoid breadth (98·5 in F 3668).

A similar reduction in the lower incisors in the male is indicated by the extremely small space between the alveoli of the canines in the mandibular fragment (s., above). In the female, the upper incisors are well-preserved in M 18720, where it can be seen that they were, even when unworn, considerably smaller than those of other large Cercopithecinae, relative to the size of the animal. The lower incisors, finely preserved in F 3398, are also small and slender.

The dimensions of the cheek-teeth are shown in Table 4.

TABLE 4

Dimensions of Cheek-Teeth in *Theropithecus*

	KNOWN MALES				KNOWN FEMALES				WHOLE SAMPLE	
	N	Mean	Range	s^2	N	Mean	Range	s^2	N	Range
P^3 Breadth										
Theropith. gelada	10	7·15	6·4– 8·0	0·176	1	6·2	—	—	11	6·2– 8·0
Kanjera	1	10·7	—	—	2	8·7	8·6– 8·8	—	3	8·6–10·7
Olorgesailie	—	10·5	—	—	—	—	—	—	12	9·6–10·7
Makapan	—	—	—	—	1	7·7	—	—	1	7·7
Swartkrans	—	—	—	—	3	9·3	8·9–10·0	0·240	5	8·9–10·0
P^3 Length										
T. gelada	10	6·4	6·2– 6·8	0·038	1	4·9	—	—	11	4·9– 6·8
Kanjera	1	8·0	—	—	2	6·7	6·4– 7·0	—	3	6·4– 8·0
Olorgesailie	1	8·5	—	—	—	—	—	—	12	8·1–10·4
Makapan	—	—	—	—	1	5·7	—	—	1	5·7
Swartkrans	—	—	—	—	3	8·0	6·0– 9·6	2·240	5	6·0–11·3
P^3EUL										
Kanjera	1	8·4	—	—	2	7·4	7·2– 7·6	—	3	7·2– 8·4
Olorgesailie	1	8·5	—	—	—	—	—	—	12	8·1–10·4
P^4 *Breadth*										
T. gelada	10	7·7	7·0– 8·7	0·294	1	6·6	—	—	11	6·6– 8·7
Kanjera	1	10·8	—	—	3	9·8	9·6– 9·9	0·02	3	9·6–10·8
Olorgesailie	1	13·7	—	—	—	—	—	—	6	11·0–13·7
Makapan	—	—	—	—	2	8·7	8·6– 8·8	—	2	8·6– 8·8
Swartkrans	—	—	—	—	3	9·9	9·0–10·6	0·435	6	9·0–10·7
P^4 Length										
T. gelada	10	6·86	6·1– 7·3	0·123	1	5·7	—	—	11	5·7– 7·3
Kanjera	1	8·7	—	—	3	7·9	7·7– 8·1	0·09	3	7·7– 8·1
Olorgesailie	1	8·5	—	—	—	—	—	—	6	8·5–10·4
Makapan	—	—	—	—	2	7·65	7·5– 7·8	—	2	7·5– 7·8
Swartkrans	—	—	—	—	3	8·1	7·3– 9·2	0·63	6	7·3– 9·5
P^4EUL										
Kanjera	1	9·4	—	—	3	8·6	8·3– 8·7	0·04	3	8·3– 8·7
Olorgesailie	1	8·5	—	—	—	—	—	—	6	8·5–10·4

TABLE 4 (continued)

	KNOWN MALES				KNOWN FEMALES				WHOLE SAMPLE	
	N	Mean	Range	s^2	N	Mean	Range	s^2	N	Range
M^1 Anterior Breadth										
T. gelada	10	9·1	8·7– 9·4	0·059	—	—	—	—	10	8·7– 9·4
Kanjera	1	12·8	—	—	3	10·5	10·2–11·0	1·51	6	10·2–12·8
Olorgesailie	1	15·3	—	—	—	—	—	—	8	13·2–15·3
Makapan	—	—	—	—	1	9·9	—	—	1	9·9
Swartkrans	—	—	—	—	3	11·26	10·9–12·0	0·284	4	10·9–12·0
Hopefield	—	—	—	—	—	—	—	—	2	9·9–14·0
M^1 Posterior Breadth										
T. gelada	10	8·5	8·1– 9·1	0·074	—	—	—	—	10	8·1– 9·1
Kanjera	1	12·3	—	—	3	10·0	9·8–10·3	0·06	6	9·8–12·3
Olorgesailie	1	14·7	—	—	—	—	—	—	8	12·9–14·7
Makapan	—	—	—	—	1	9·4	—	—	1	9·4
Swartkrans	—	—	—	—	3	10·4	9·9–10·6	0·126	4	9·9–10·6
Hopefield	—	—	—	—	—	—	—	—	2	9·5–12·5
M^1 Length										
T. gelada	10	10·5	9·9–11·2	0·156	—	—	—	—	10	9·9–11·2
Kanjera	1	13·1	—	—	3	10·8	10·4–11·1	0·086	6	10·4–13·1
Olorgesailie	1	15·5	—	—	—	—	—	—	8	15·5–17·5
Makapan	—	—	—	—	1	12·0	—	—	1	12·0
Swartkrans	—	—	—	—	3	13·2	12·0–15·1	1·913	4	11·7–15·1
Hopefield	—	—	—	—	—	—	—	—	2	12·0–14·0
M^1 EUL										
Kanjera	1	14·0	—	—	3	12·8	12·5–13·1	0·079	6	12·5–14·0
Olorgesailie	1	16·5	—	—	—	—	—	—	8	16·1–17·6
M^2 Ant. Breadth										
T. gelada	10	11·0	10·0–11·6	0·166	1	9·7	—	—	11	9·7–11·6
Kanjera	1	14·8	—	—	3	12·8	12·3–13·0	0·235	5	12·3–14·8
Olorgesailie	—	—	—	—	—	—	—	—	10	15·0–19·0
Makapan	—	—	—	—	—	—	—	—	2	13·3–14·9
Swartkrans	—	—	—	—	3	13·9	13·6–14·5	2·00	5	13·6–14·9
Kaiso	—	—	—	—	—	—	—	—	1	12·5
M^2 Post. Breadth										
T. gelada	10	9·8	9·3–10·3	0·146	1	8·5	—	—	11	8·5–10·3
Kanjera	1	14·2	—	—	3	11·7	11·4–12·2	0·194	5	11·4–14·2
Olorgesailie	—	—	—	—	—	—	—	—	10	13·5–17·4
Makapan	—	—	—	—	—	—	—	—	2	12·8–13·6
Swartkrans	—	—	—	—	3	12·66	12·3–13·2	0·318	5	12·3–13·3
Kaiso	—	—	—	—	—	—	—	—	1	12·0
M^2 Length										
T. gelada	10	12·8	11·4–13·7	0·522	1	11·0	—	—	11	11·0–13·7
Kanjera	1	17·7	—	—	3	14·4	14·2–15·1	0·249	5	14·0–17·7
Olorgesailie	—	—	—	—	—	—	—	—	10	18·7–22·3
Makapan	—	—	—	—	—	—	—	—	2	16·8–17·9
Swartkrans	—	—	—	—	3	17·3	16·6–18·1	0·380	5	15·9–18·1
Kaiso	—	—	—	—	—	—	—	—	1	15·4

TABLE 4 (continued)

	KNOWN MALES				KNOWN FEMALES				WHOLE SAMPLE	
	N	Mean	Range	s^2	N	Mean	Range	s^2	N	Range
M^2 EUL										
Kanjera	1	18·1	—	—	3	15·5	15·2–15·8	0·060	5	15·2–18·4
Olorgesailie	—	—	—	—	—	—	—	—	10	18·9–23·0
Kaiso	—	—	—	—	—	—	—	—	1	16·3
M^3 Ant. Breadth										
T. gelada	9	11·1	10·2–12·4	0·326	1	9·2	—	—	10	9·2–12·4
Kanjera	1	14·3	—	—	3	13·2	12·9–13·5	0·148	6	12·9–14·3
Olorgesailie	—	—	—	—	—	—	—	—	8	15·7–18·0
Makapan	—	—	—	—	—	—	—	—	2	12·7
Swartkrans	—	—	—	—	1	14·2	—	—	2	14·0–14·2
Kaiso	—	—	—	—	—	—	—	—	1	13·3
M^3 Post. Breadth										
T. gelada	9	9·6	8·8–10·3	0·193	1	8·0	—	—	10	8·0–10·3
Kanjera	1	12·8	—	—	3	10·9	10·4–11·2	0·137	6	10·4–12·8
Olorgesailie	—	—	—	—	—	—	—	—	8	13·8–15·9
Makapan	—	—	—	—	—	—	—	—	2	10·2–12·2
Swartkrans	—	—	—	—	1	12·3	—		2	12·2–12·3
Kaiso	—	—	—	—	—	—	—	—	1	11·3
M^3 Length										
T. gelada	9	13·2	11·9–14·0	0·490	1	11·5	—	—	10	11·5–14·0
Kanjera	1	18·1	—	—	3	15·8	14·6–16·6	0·744	6	14·6–18·1
Olorgesailie	—	—	—	—	—	—	—	—	8	18·6–22·5
Makapan	—	—	—	—	—	—	—	—	2	16·9–19·1
Swartkrans	—	—	—	—	1	17·6	—	—	2	16·6–17·6
Kaiso	—	—	—	—	—	—	—	—	1	17·3
M^3 EUL										
Kanjera	1	18·1	—	—	3	16·1	15·2–16·8	0·446	6	15·2–18·1
Olorgesailie	—	—	—	—	—	—	—	—	8	19·0–23·0
Kaiso	—	—	—	—	—	—	—	—	1	17·3
P_3 Breadth										
T. gelada	9	5·1	4·6– 5·4	0·063	1	4·0	—	—		
Kanjera	2	7·05	6·8– 7·3	—	4	6·35	5·9– 6·8	0·103	(All sexed)	
Olorgesailie	5	8·1	7·5– 8·6	0·246	6	6·65	6·2– 7·4	0·166	,,	
Makapan	2	7·0	7·0	—	—	—	—	—	,,	
Swartkrans	2	7·2	6·6– 7·8	0·36	2	5·8	5·6– 6·0	—	,,	
P_3 Length										
T. gelada	9	18·7	17·1–20·4	0·927	1	8·9	—	—	(All sexed)	
Kanjera	1	20·3	—	—	4	12·4	11·4–13·8	2·063	,,	
Olorgesailie	5	19·9	18·3–20·7	0·780	6	12·8	12·0–14·0	0·49	,,	
Makapan	2	24·2	23·4–25·0	0·64	—	—	—	—	,,	
Swartkrans	1	25·1	—	—	2	11·05	10·8–11·3	—	,,	

TABLE 4 (continued)

	KNOWN MALES				KNOWN FEMALES				WHOLE SAMPLE	
	N	Mean	Range	s^2	N	Mean	Range	s^2	N	Range
P_3 *EUL*	As Length									
P_4 *Breadth*										
T. gelada	9	6·5	6·0– 7·3	0·119	1	5·9	—	—	10	5·9– 7·3
Kanjera	—	—	—	—	2	7·9	7·8– 8·0	—	3	7·3– 8·0
Olorgesailie	2	9·5	8·8–10·2	—	1	9·6	—	—	10	8·6– 9·7
Makapan	2	8·75	8·5– 9·0	—	—	—	—	—	4	7·1– 9·0
Swartkrans	2	9·25	8·5–10·0	—	2	8·1	7·8– 8·4	—	5	7·8–10·0
Hopefield	—	—	—	—	—	—	—	—	1	9·9
P_4 *Length*										
T. gelada	9	7·5	6·7– 7·9	0·164	1	6·6	—	—	10	6·6
Kanjera	—	—	—	—	2	8·95	8·7– 9·2	—	3	8·7– 9·4
Olorgesailie	2	11·0	10·0–12·0	—	1	10·0	—	—	10	10·0–12·0
Makapan	2	9·5	9·0–10·0	—	—	—	—	—	4	8·2–10·4
Swartkrans	2	11·4	10·8–12·0	—	2	9·15	9·4– 9·5	—	5	9·4–12·0
Hopefield	—	—	—	—	—	—	—	—	1	(11·1)
P_4 *EUL*										
Kanjera	—	—	—	—	2	9·4	9·2– 9·6	—	3	9·2– 9·6
Olorgesailie	2	11·0	10·0–12·0	—	1	10·0	—	—	10	10·0–12.0
M_1 *Ant. Breadth*										
T. gelada	9	7·5	7·2–7·9	0·156	1	6·7	—	—	10	6·7– 7·9
Kanjera	—	—	—	—	3	9·2	8·8– 9·9	0·291	5	8·8– 9·9
Olorgesailie	—	—	—	—	1	11·5	—	—	12	10·5–12·6
Makapan	1	9·5	—	—	—	—	—	—	1	9·5
Swartkrans	1	11·8	—	—	2	10·3	10·1–10·5	—	4	9·8–11·8
Hopefield	—	—	—	—	—	—	—	—	1	9·7
M_1 *Post. Breadth*										
T. gelada	8	7·7	7·2– 8·2	0·075	1	7·1	—	—	9	7·1– 8·2
Kanjera	—	—	—	—	3	9·3	9·0– 9·9	0·200	5	8·6– 9·9
Olorgesailie	1	12·9	—	—	1	10·5	—	—	12	
Makapan	1	9·6	—	—	1	9·0	—	—	2	9·0—9·6
Swartkrans	1	12·3	—	—	2	11·3	11·2–11·4	—	4	10·0–12·3
Hopefield	—	—	—	—	—	—	—	—	1	9·9
M_1 *Length*										
T. gelada	9	10·1	9·5–10·5	0·287	1	9·3	—	—	10	9·3–10·5
Kanjera	—	—	—	—	3	11·2	10·1–12·9	1·544	5	10·1–12·9
Olorgesailie	—	—	—	—	1	14·4	—	—	12	14·4–16·5
Makapan	1	11·8	—	—	1	9·6	—	—	2	9·6–11·8
Swartkrans	1	15·8	—	—	2	11·75	11·3–12·2	—	4	11·3–15·8
Hopefield	—	—	—	—	—	—	—	—	1	(13·8)

TABLE 4 (continued)

	KNOWN MALES				KNOWN FEMALES				WHOLE SAMPLE	
	N	Mean	Range	s^2	N	Mean	Range	s^2	N	Range
M_1 EUL										
Kanjera	—	—	—	—	3	12·9	12·8–13·2	0·044	5	11·9–14·0
Olorgesailie	—	—	—	—	1	15·5	—	—	12	15·5–17·0
M_2 Ant. Breadth										
T. gelada	9	9·3	8·8–10·0	0·117	1	8·1	—	—	10	8·1–10·0
Kanjera	—	—	—	—	3	11·6	11·5–11·8	0·02	5	11·5–12·5
Olorgesailie	1	16·0	—	—	1	12·8	—	—	8	12·8–16·0
Makapan	1	12·3	—	—	1	11·2	—	—	2	11·2–12·3
Swartkrans	2	13·2	12·3–14·1	—	2	12·75	12·7–12·8	—	6	12·2–14·1
Hopefield	—	—	—	—	—	—	—	—	1	14·0
M_2 Post. Breadth										
T. gelada	9	8·9	8·0– 9·5	0·252	1	8·1	—	—	10	8·0– 9·5
Kanjera	—	—	—	—	3	11·2	11·1–11·3	0·006	5	11·1–11·5
Olorgesailie	1	15·0	—	—	1	13·3	—	—	8	12·4–15·0
Makapan	1	12·1	—	—	1	11·2	—	—	2	11·2–12·1
Swartkrans	2	12·9	12·0–13·8	—	2	12·45	12·4–12·5	—	6	11·7–13·8
Hopefield	—	—	—	—	—	—	—	—	1	15·0
M_2 Length										
T. gelada	9	12·7	11·9–13·5	0·185	1	11·1	—	—	10	11·1–13·5
Kanjera	—	—	—	—	3	14·9	13·8–15·5	0·595	5	13·8–15·5
Olorgesailie	1	22·5	—	—	1	17·2	—	—	8	17·2–22·5
Makapan	1	15·9	—	—	1	13·1	—	—	2	13·1–15·9
Swartkrans	2	18·7	17·1–20·3	—	2	15·5	15·4–15·6	—	6	14·8–17·3
Hopefield	—	—	—	—	—	—	—	—	1	16·5
M_2 EUL										
Kanjera	—	—	—	—	3	15·6	15·5–15·6	0·023	5	15·5–15·9
Olorgesailie	1	22·25	—	—	1	18·2	—	—	8	17·2–22·5
M_3 Ant. Breadth										
T. gelada	8	9·95	9·2–10·7	0·227	1	8·5	—	—	9	8·5–10·7
Kanjera	—	—	—	—	1	12·1	—	—	6	11·7–13·5
Olorgesailie	—	—	—	—	1	15·9	—	—	8	15·1–17·2
Makapan	1	13·2	—	—	1	12·1	—	—	2	12·1–13·2
Swartkrans	1	14·7	—	—	2	13·6	13·4–13·8	—	5	13·1–16·5
Hopefield	—	—	—	—	—	—	—	—	1	18·0
M_3 Post. Breadth										
T. gelada	8	9·1	8·2– 9·5	0·205	1	8·0	—	—	9	8·0– 9·5
Kanjera	—	—	—	—	1	11·3	—	—	6	11·3–12·0
Olorgesailie	—	—	—	—	1	14·5	—	—	8	13·2–15·6
Makapan	1	12·1	—	—	1	10·8	—	—	2	10·8–12·1
Swartkrans	1	13·3	—	—	2	12·45	12·0–12·9	—	5	12·0–15·2
Hopefield	—	—	—	—	—	—	—	—	1	16·5

Table 4 (continued)

	KNOWN MALES				KNOWN FEMALES				WHOLE SAMPLE	
	N	Mean	Range	s^2	N	Mean	Range	s^2	N	Range
M_3 Length										
T. gelada	8	16·6	16·0–17·2	0·194	1	14·0	—	—	9	14·0–17·2
Kanjera	—	—	—	—	1	20·0	—	—	6	19·8–23·2
Olorgesailie	—	—	—	—	1	24·7	—	—	8	23·7–27·3
Makapan	1	21·0	—	—	1	18·9	—	—	2	18·9–21·0
Swartkrans	1	26·5	—	—	2	21·4	20·1–22·7	—	5	20·1–26·5
Hopefield	—	—	—	—	—	—	—	—	1	26·8
M_3 EUL										
Kanjera	—	—	—	—	1	20·1	—	—	6	20·0–23·5
Olorgesailie	—	—	—	—	1	24·7	—	—	8	23·7–27·3

Cheek-tooth dimensions in Olduvai *Simopithecus*

No.	Site/Bed	Sex	Tooth	Ant. Br.	Post. Br.	Length	EUL
301	BK II	?	M^1	13·8	12·7	15·2	15·8
262	SHK II	?	M^1	12·4	(12·9)	13·2	(15·1)
622	SHK II	?	M^1	13·1	(12·5)	12·1	(14·7)
M 14939	II	?	M^2	16·2	15·0	20·9	21·0
1091	BK II	?	M^2	14·6	14·1	19·0	19·4
M 14681	?	?	M^2	14·4	13·9	16·3	17·0
,,	?	?	M^3	14·0	12·4	18·0	19·0
1096	BK II	?	M^3	17·1	14·5	22·5	23·0
436	BK II	?	M^3	16·8	13·7	21·3	21·3
M 14953	II	F	M_1	11·8	10·7	11·0	12·2
,,	,,	,,	M_2	13·3	12·8	17·1	17·5
,,	,,	,,	M_3	14·4	13·0	24·1	24·1
M 14937	DKI	?	M_1	9·0	9·8	10·3	(12·0)
,,	,,	?	M_2	11·8	11·3	14·5	15·4
,,	,,	?	M_3	13·5	12·3	20·2	20·5
Juv. (no no.)	BK II	F	M_1	11·0	11·4	14·5	14·7
,,	,,	,,	M_2	12·6	12·4	17·8	18·1
Ex. 117	,,	?	M_2	13·7	12·6	16·6	17·6
200	BK II	?	M_2	13·7	13·1	19·1	19·2
694	GRC	?	M_2	14·2	13·7	18·4	18·5
1332	GRC	?	M_3	14·3	13·6	24·9	25·1
'Olduvai'	?	?	M_3	14·7	12·7	23·5	23·9
M 14938	DKI	F	M_3	14·7	12·6	21·9	22·2
M 14680	IV	M	M_1	12·0	12·0	16·4	16·4
,,	,,	,,	M_2	16·2	15·1	21·1	21·1
580, 57	JLK IV	F	M_1	11·3	11·1	13·6	15·5
,,	,,	,,	M_2	15·7	13·6	17·0	18·9
,,	,,	,,	M_3	16·6	14·0	23·8	24·0

TABLE 4 (continued)

No.	Site/Bed	Sex	Tooth	Breadth	Length	EUL
M 18779	II	F	P^3	10·1	8·2	8·2
,,	,,	,,	P^4	11·4	9·9	9·9
M 14938	DKI	F	P_3	5·8	13·0	13·3
,,	,,	,,	P_4	7·4	10·6	10·8
Juv.	BK II	F	P_3	7·1	13·4	13·4
,,	,,	,,	P_4	8·5	10·5	10·5
M 14680	IV	M	P_3	9·4	17·7	17·7
,,	,,	,,	P_4	11·2	12·8	12·8
580,57	JLK IV	F	P_3	(8·5)	(12·0)	?
,,	,,	,,	P_4	10·5	11·5	(12·0)

Forelimb

The *scapula* is represented by four fragmentary specimens, all undescribed and unregistered (Plate 11a and b):

1. A fragment of a left acromion, excluding the extreme tip.
2. A fragment of the distal end of a right scapula, including the posterior part of the glenoid cavity, a short length of the anterior border, and the acromion.
3. A larger fragment consisting of the glenoid region, part of the cranial and axillary margins, the base of the acromion, and the adjoining part of the spine, of which the free edge is absent.
4. An isolated left glenoid region, with a small portion of the neck and the axillary border.

The dimensions of the specimens are shown in Table 5. The areas of origin of the

TABLE 5

Dimensions of scapula in *Simopithecus* and representative specimens of extant species

Dimensions: a. Breadth across acromion and glenoid fossa
b. Breadth of glenoid articular surface
c. Height of glenoid articular surface.

Site/Species and Specimen No.	No. in descriptive list	Known or probable sex	Dimensions a.	b.	c.
Kanjera	2	?	47·5	22·5	
	3	?	—	22·5	30
	4	?	—	23·5	33
Olorgesailie		?	—	(29)	(35)
		?	—	(29·5)	(41)
		?	—	27	39
T. gelada AMNH 60568	–	M	40	17	23
U. primatol.	–	M	41	17	22
P. anubis AMNH 82097	–	M	46	19	27
AMNH 82096	–	F	37	16	24·5
Pan USNM 176230	–	M	49	24	31
USNM 176227	–	F	45	23	28
Gorilla USNM 239883	–	M	78	40	56
USNM 220060	–	F	53	29	35

spino- and acromio-deltoid muscles agree with the condition in living genera. The acromion itself is rather short and stout, and also oriented as in the terrestrial rather than the arboreal modern genera. The neck is rather broad, indicating a stout and heavy build. The areas of origin of the round and aponeurotic portions of M. triceps, caput longum, are strongly-marked. The spino-glenoid notch is deep.

The *humerus* is represented by eleven specimens, of which seven are new, and which between them represent the whole bone (Plate 11c, d and e):

1. Part of the proximal end of a right humerus, from the surgical neck to the level of the midpoint of the delto-pectoral crest. An isolated head with part of the lesser tuberosity makes a good fit with the posterior part of its broken proximal surface.
2. Part of the shaft of a left humerus, showing the anterior surface in the region of the deltoid insertion.
3. M 18791. Part of a left humeral shaft, from just above the midpoint of the insertion of M. teres major to well below the delto-pectoral crest.
4. A fragment of a left shaft, almost exactly as the last, but less complete distally.

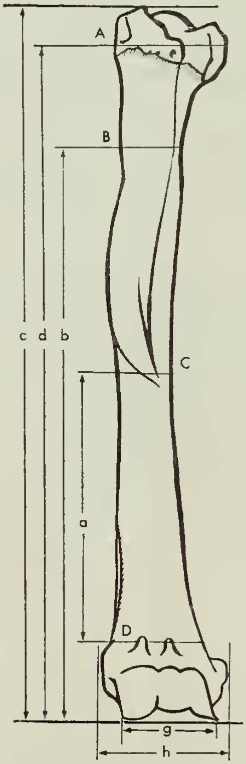


FIG. 4. Anterior aspect of humerus, showing dimensions quoted in Table 6. A. Horizontal plane at most proximal point of diaphysis. B. Plane at midpoint of insertion of M. teres major tendon. C. Plane where deltoid crest crosses anterior margin. D. Plane immediately proximal to tubercle of insertion of M. extensor radialis longus.

5. The distal part of a right shaft, with the distal end of the deltoid insertion, broken distally just proximal to the anconeal fossa.

6. Fragment of the distal end of a humeral shaft, broken distally as No. 5, proximally just above the upper end of the brachioradialis crest.

7. Fragment resembling No. 5, but with less preserved both proximally and distally.

8. M 11542. Fragment of a left humerus, well-preserved distal to the level of the insertion of M. teres major, but with most of the deltopectoral crest and the radial epicondyle broken away.

9. M 18789. The complete distal extremity of a right humerus.

10. M 11543. The distal part of a left humerus, much as No. 8, but more complete anteriorly.

11. M 18721. The distal part of a left humerus, the posterior surface preserved from above the level of the distal end of the deltoid insertion, the anterior surface broken in this region, but preserved distally.

Dimensions are shown in Table 6.

In none of the specimens is the greater tuberosity preserved, so that its projection beyond the level of the head, an indication of terrestrial adaptation (Jolly, 1967) cannot be determined. The head itself (one specimen) appears to be rather flatter, less hemispherical, than in any of the living Cercopithecoidea, but this feature is not easy to measure objectively. In all the nine specimens in which the region is preserved, the area of origin of M. brachialis extends broadly on to the posterior surface, thus agreeing with all the modern Cercopithecinae examined except the single specimen of *Theropithecus gelada* dissected. This can be deduced from the position of the raised line dividing the area of origin of the brachialis from that of triceps, and from the presence of a distinct line running between the prominent deltoid-triceps-brachialis crest and the large triceps lateralis rugosity on the lateral aspect of the proximal end.

The region of the lateral epicondylar ridge is preserved wholly or partly in seven specimens. In none is it raised prominently above the profile of the lateral margin of the humerus, as it is in the large climbing forms *Macaca* and *Mandrillus*, which have powerful Mm. brachialis and brachioradialis.

The third reliable indicator of terrestrial adaptation, the relative breadth of the distal articular surface expresses the relative size of the epicondyles, especially the ulnar, which is large and prominent in arboreal monkeys (Jolly, 1967).

The dimensions of overall distal breadth and articular breadth of three Kanjera specimens are plotted in Fig. 5 together with those of the modern series. With indices (100 × articular breadth/bi-epicondylar breadth) of 70·8, 71·7 and 75·0, these lie beyond the range of the arboreal series, and with the modern baboons.

Judging by size Nos 1, 4, 6, 8, 9 are from male individuals, 3, 5, 10, 11 from females. Nos 1 and 9 are possibly parts of the same humerus, while 8 is closely similar in size, and may well be its pair. The midpoint of the insertion of M. teres major occurs on both 1 and 8, enabling the approximate overall length of the male humerus to be estimated (236 mm). The unbroken length of No. 8 can be estimated from the

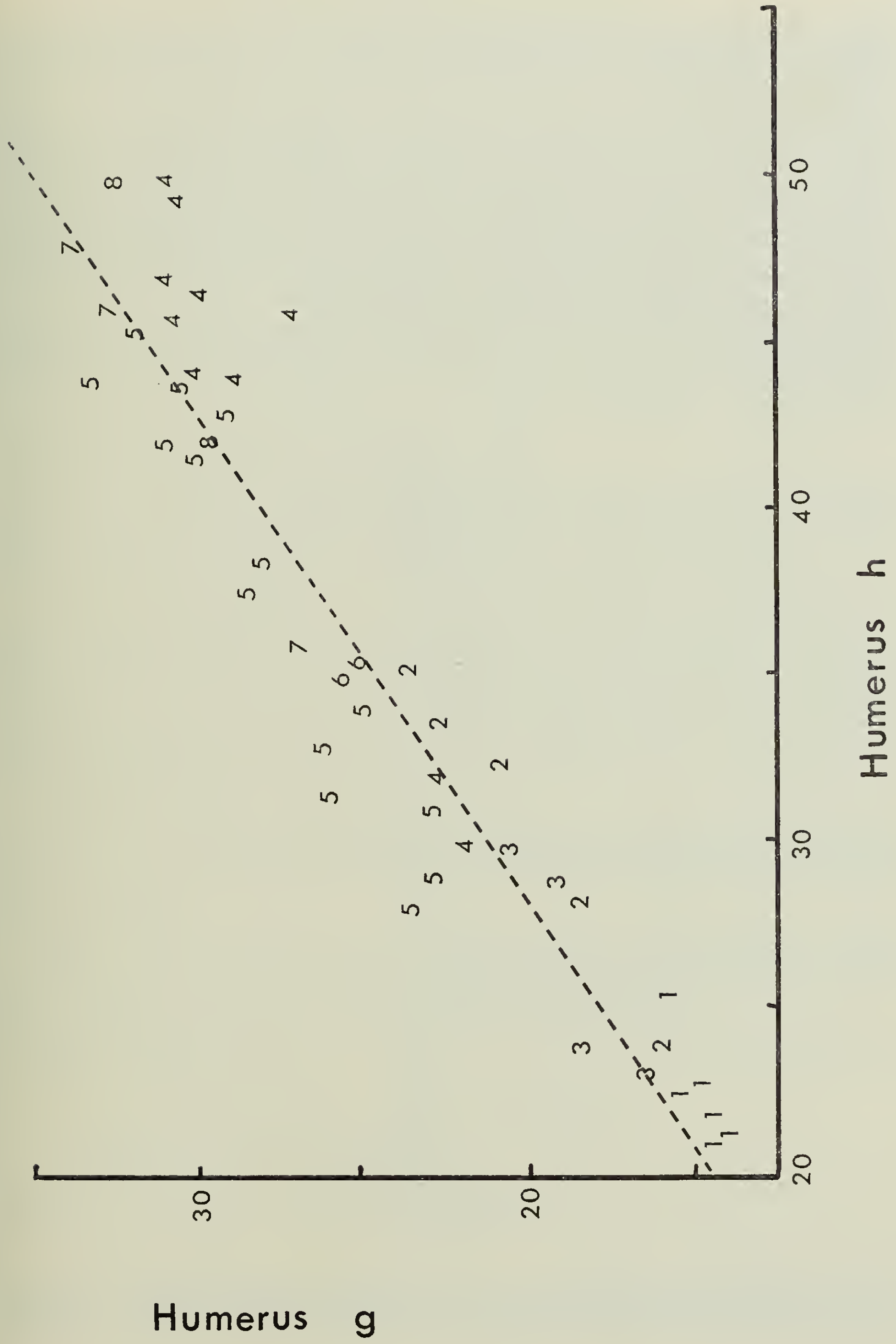
TABLE 6

Dimensions of humerus in *Simopithecus* and representative specimens of extant species
For Dimensions a–d see Fig. 4.

e. Transverse diameter at B (Fig. 4)
f. Transverse diameter at D (Fig. 4)
g. Breadth of distal articular surface
h. Bi-epicondylar breadth
i. Antero-posterior diameter at B (Fig. 4)
j. Antero-posterior diameter at C (Fig. 4)
k. Minimum antero-posterior diameter of trochlear surface.

Site/Species and Specimen No.	No. in Descriptive list	Known or Probable Sex	Dimensions (see Fig. 4)										
			a.	b.	c.	d.	e.	f.	g.	h.	i.	j.	k.
Kanjera	1	(M)	—	—	—	—	20	—	—	—	25·5	—	—
M 18791	3	(F)	—	—	—	—	16	—	—	—	19·5	18	—
—	4	(M)	—	—	—	—	19·5	—	—	—	23	22	—
—	5	(F)	80	—	—	—	—	24·5	—	—	—	17	—
—	6	(M)	—	—	—	—	—	32	—	—	—	—	—
M 11542	8	(M)	92	178·5	—	—	20	33	34	48	—	22·5	17
M 18789	9	(M)	—	—	—	—	—	34	33	46	—	—	17
M 11543	10	(F)	66	140·5	—	—	14·5	29	27	36	19	16	14
M 18721	11	(F)	—	—	—	—	—	29	26	—	—	—	13·5
Olorgesailie													
2993	1	(M)	100	226	—	267	23	46	44	62	28	28	(20)
FUI/UL	4	?	—	—	—	—	—	—	(34)	—	—	—	17
FU2/UL	5	(F)	—	—	—	—	—	—	(36·5)	—	—	—	20
FU3/UL	6	(?F)	—	—	—	—	—	—	36	—	—	—	18
Olduvai													
1384 BK II E	1	?	104·5	—	—	—	—	37·5	29·5	42	-	22·5	14
BK II 118	2	?	91	(172)	—	—	—	32	—	—	—	18	16
SWK F2953	3	?	—	—	—	—	—	—	32·5	50	—	—	16
T. gelada													
U. Primatol.	—	M	79·5	148	194	—	15	25	22·5	36·5	17	17	14
AMNH 60568	—	M	87	161	204	193	17·5	25	25	36	17	16·5	13
P. anubis													
AMNH 82097	—	M	98	189	245	234	16	35	30	45	19	21	15
AMNH 82096	—	F	83·5	156	206	199	15	29	26	34·5	18	18	14
Pan													
USNM 176230	—	M	116	254	325	304	25	50	46	64	22	23	19
USNM 176227	—	F	108	201	283	264	22	43	42	58	22	22	15
Gorilla													
USNM 239883	—	M	128	302	424	—	39	84	72	106	40	36	23
USNM 220060	—	F	125	258	360	—	24	50	49	69	24	23	18

FIG. 5. Proportions of the distal end of the humerus in Cercopithecinae. Dimensions as shown in Fig. 4. 1. *Cercopithecus*. 2. *Macaca*. 3. *Cercocebus*. 4. *Mandrillus*. 5. *Papio*. 6. *T. gelada*. 7. *Simopithecus* (Kanjera). 8. *Simopithecus* (Olduvai).



c

value of the expression: overall length/length midpoint M. teres major insertion to capitulum, obtained from a *Theropithecus gelada* humerus. This gives a closely similar value, 233 mm.

The same formula may be used to calculate the unbroken length of the small female specimen (10). A value of 184 mm is obtained using gelada proportions, 186 mm using the reconstructed length of the male humerus. However, No. 10 is consistently the smallest specimen of the female series. Anterior-posterior breadth at the distal end of the deltoid crest averages 17 mm and ranges up to 18 mm. in the limited female sample. If length varied in proportion, it would have been about 196 mm in an average, and 209 mm in a large female.

All six specimens of the *radius* are registered in the British Museum collection (Plate 12d and e).

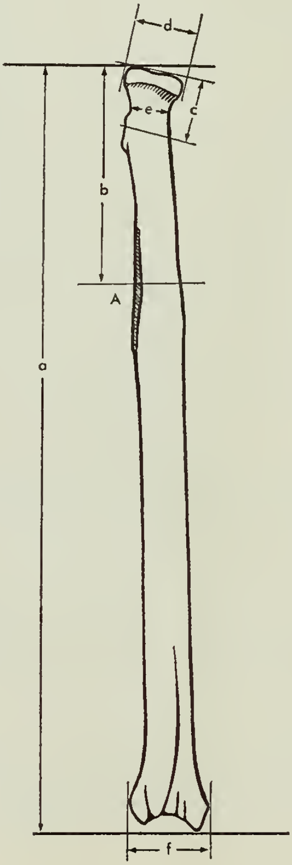


Fig. 6. Posterior aspect of radius, showing dimensions quoted in Table 7. A. Horizontal plane bisecting area of attachment of strong, oblique part of interosseous ligament.

1. M 11544. A left radius, with all the surface details well-preserved, complete apart from some slight erosion of the head. The details of the surface resemble those seen in *Theropithecus gelada* rather closely, but the muscular moulding of the shaft is stronger and the interosseous border rather more prominent. The area corresponding to the attachment of the strong, oblique part of the interosseous membrane is distinguishable, and a small, roughened area on the volar surface, immediately distal to the bicipital tuberosity, probably represents the origin of the M. abductor pollicis longus. The crest separating the positions of the extensors and abductor pollicis longus in the distal third of the shaft is prominent, but rounded, as in *Theropithecus gelada*, without the lipping frequently present in more arboreal monkeys. The shaft has slight posterior convexity, and rather greater lateral convexity than is seen in *Theropithecus gelada* and the more gracile forms of *Papio*, resembling the more heavily built forms of *Papio*, and *Mandrillus*. The morphology of the distal extremity resembles that of *Theropithecus gelada*. From its size, the specimen probably represents a female individual.

2–6. The remaining specimens of the radius, which are heads with variable amounts of shaft preserved (M 18801, 18802, 18717, 18716, 11545) agree in structure with M 11544, especially in the deep excavation of the volar surface and the prominence of the interosseous border. Their dimensions are shown in Table 7.

The size of the specimens, so far as this can be gauged from the breadth of the head and neck, indicates that 2, 3 and 5 are from males, and 1, 4 and 6 from females. The overall length of No. 1 is 198 mm. This was evidently from a large female; the mean of neck breadth in the female series is 12·3 mm, and the lowest value 12·0 mm (94·6 and 92·3%, respectively, of the neck breadth of No. 1). If their length was proportionately less than that of No. 1, this would have been about 187 mm in an average, and 183 mm in a small female.

The unbroken length of the male fragment No. 2 can be estimated from the proportions of the whole female radius (No. 1) by using the formula: total length/length from head of midpoint of insertion of the strong, oblique part of the interosseous membrane.

This gives a value of 224 mm for No. 2, the largest of the male fragments. Adjusting this value with reference to neck breadth allows an estimate of 216 mm for radius length in average-sized males, and 208 mm in small ones.

Eight specimens of the *ulna* are present in the Kanjera collection, of which one is unregistered (Plate 12a–c).

1. M 11546. Complete apart from the distal epiphysis.
2. A fragment of shaft (unregistered).

3–8. M 18722, 18723, 18724, 18725, 18726, 18803. Proximal ends with a variable amount of shaft attached.

In all the specimens, the interosseous line is prominent. The details of morphology of the proximal end are somewhat variable, especially the degree of excavation of the medial surface. In all the specimens, the articular surface of the anconeal

Table 7

Dimensions of radius in *Simopithecus* and representative specimens of extant species

a. Radial length
b. As in Fig. 6
c. Distance from head to midpoint of bicipital tuberosity, parallel to axis of neck
d. Maximum diameter of radial head
e. Minimum value of greatest diameter of radial neck
f. Maximum breadth, distal end.

Site/Species and Specimen No.	No. in descriptive list	Known or (probable) sex	Dimensions					
			a.	b.	c.	d.	e.	f.
Kanjera								
M 11544	1	(F)	198	79	24·5	16·5	12·5	23
M 18801	2	(M)	—	88·5	29	22·5	15	—
M 18802	3	(M)		—	29	22	14·5	—
M 18717	4	(F)	—	—	20·5	17	12	—
M 18716	5	(M)	—	—	25·5	20·5	14	—
M 11545	6	(F)	—	—	19	17	12	—
Olorgesailie		?	—	—	—	21·5	—	—
OG–1463		?	—	—	—	—	—	30
OG–1462		?	—	—	—	—	—	—
Olduvai								
IS 1941	1	(?F)	—	—	25	21·5	16	—
BK II 1953/4	2	(?M)	—	—	36	25	17·5	—
Hopefield	—	?	—	—	—	19	—	—
T. gelada								
U. Primat.	—	M	210	63	19	17	12	22
AMNH 60568	—	M	220	63	19	17	12	19
P. anubis								
AMNH 82097	—	M	243	65	28	20	14	27
AMNH 82096	—	F	210	55·5	23·5	17·5	12	22·5
Pan								
USNM 176230	—	M	305	—	40	27	14	33
USNM 176227	—	F	266	—	40	22	14	34
Gorilla								
USNM 239883	—	M	364	126	68	36	19	57
USNM 220060	—	F	285	94	52	95	15	38

process faces markedly more laterally and distally than medially; in extreme specimens such as M 18723 no medially-facing part is present. The markings representing the attachments of the M. brachialis and of the humero-ulnar ligament are clearly visible in all specimens in which the coronoid process is preserved. In the unregistered shaft fragment three longitudinal raised lines are present, probably representing the interosseous line, the ridge from which the M. extensor pollicis longus and extensors of the second and third digits originate, and the fascial line dividing the latter muscle-group from the M. extensor carpi ulnaris.

In all eight specimens in which the olecranon is preserved, it is massive and obviously backwardly-reflexed in the manner typical of *Papio* and *Theropithecus gelada*. In three specimens (M 18724, M 18726, M 11564) sufficient of the shaft is preserved to permit determination of the olecranon/shaft angle (Jolly, 1967). The values obtained (60°, 73°, 50°) lie well above the upper limit for all modern genera apart from

FIG. 7. Lateral aspect of ulna, showing dimensions quoted in Table 8. A. Centre of rotation of humeral articulation. B. Centre of rotation of ulnar head.

TABLE 8

Dimensions of the ulna in *Simopithecus* and representative specimens of extant species

a. Distance from tip of coronoid process to tip of anconeal process
b. Minimum antero-posterior diameter in humeral articulation
c. Distance along AC from A to distal epiphyseal line (Fig. 7)
d. Length AC (Fig. 7).

Site/Species and Specimen No.	No. in descriptive list	Known or (probable) sex	Dimensions a.	b.	c.	d.
Kanjera						
M 11546	1	(F)	18·5	19	222·5	—
M 18722	3	?	—	19	—	—
M 18723	4	(M)	21·5	19	—	—
M 18724	5	(F)	18	16·5	—	—
M 18726	7	(M)	20	21	—	—
M 18803	8	?	17	15·5	—	—
Olorgesailie	—	?	26	—	—	—
T. gelada						
U. Primat.	—	M	17	14·5	205	209
AMNH 60568	—	M	16·5	14·5	214	220
Papio anubis						
AMNH 82097	—	M	21	17	232	237
AMNH 82096	—	F	16·5	16	214·5	217
Pan						
USNM 176230	—	M	24	21	289	297
USNM 176227	—	F	20	20	252	259
Gorilla						
USNM 239883	—	M	27	34	329	349
USNM 220060	—	F	22	23	265	272

the baboons, and at the upper end of the range of these (Fig. 8). None of the specimens show the antero-posterior broadening of the shaft posterior to the humeral articulation, which is distinctive of *Mandrillus* and some specimens of the larger species of *Macaca*.

The ulnar fragments do not fall clearly into two differently-sized groups, although the massive fragments Nos 4 and 7 can safely be attributed to males, and No. 5, which is much smaller, though mature, to a female. No. 8 is small but has an unfused acromial ephiphysis. No. 1 was from an almost mature individual, since only the distal epiphysis was unfused.

Hindlimb and Axial Skeleton

The *sacrum* is represented by a single specimen (M 18715) consisting of the two proximal sacral vertebrae, with the wings somewhat damaged and the superior articular processes absent. The articular crest of both sides has been sheared off, exposing the ventral floor of the neural canal. The distal surface is smooth and articular anteriorly, but posteriorly is broken away, indicating that an incompletely fused third sacral vertebra was present, as is regularly found in large Cercopithecoidea.

The *pelvis* is represented by eight specimens (M 11547, 18711, 18712, 18713, 18714, 18792, 18804, and an unregistered fragment). Between them they include the whole innominate bone, apart from the ischial tuberosities, the crest of the ilium, and part of the pubic ramus. The pelvis of *Simopithecus* was evidently similar in shape and proportions to that of other large Cercopithecoidea.

In spite of the difference in orientation of the tail in the living animal, no consistent distinction could be demonstrated in the tilt of the sacrum on the ilium between *Papio* and *Mandrillus* and *Theropithecus gelada.*

The *femur* is represented by eight fragments, of which three are unregistered (Plate 13a–c).

1. M 18807. Head, neck and adjoining part of the shaft of a right femur.
2. M 18710. Fragment from the proximal end of a right femur, with the lesser trochanter, but without the greater trochanter, head and neck.

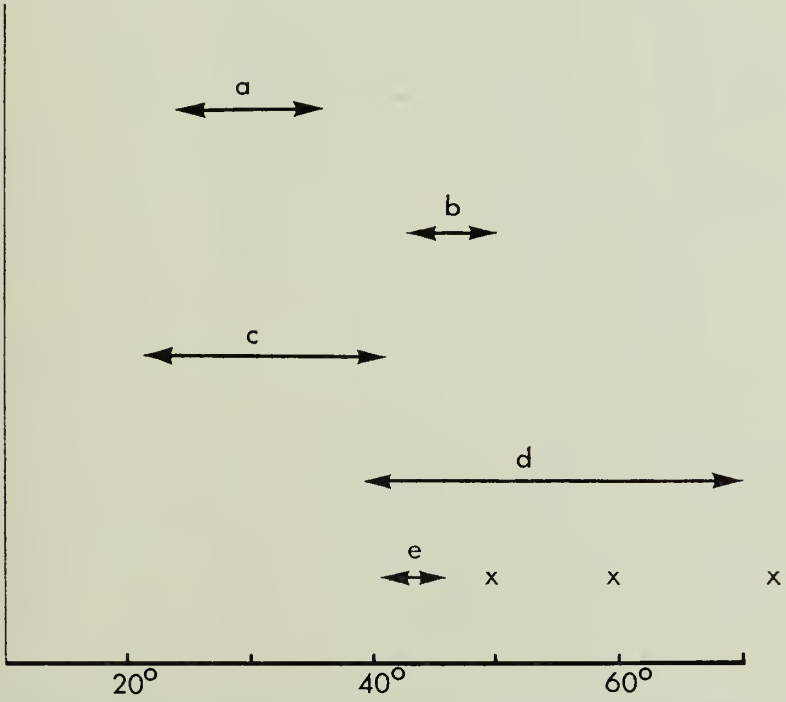


FIG. 8. Range of olecranon inclination angle in cercopithecine ulnae. Crosses represent Kanjera *Simopithecus* specimens. a. *Macaca* (N = 15). b. *Mandrillus* (N = 3). c. *Cercocebus* (N = 5). d. *Papio* (N = 24). e. *T. gelada* (N = 2).

3. M 18709. Fragment from the proximal end of a right femur, broken transversely at the level of the lesser trochanter.

4. M 11548. The greater part of a left femur, broken proximally at about midway along the intertrochanteric crest, distally at the level of the shallow pit representing the position of the bursa lying beneath the quadriceps tendon.

5. M 18708. Part of a right femur, almost exactly as the last, but with rather less of the proximal end preserved.

6. Fragment of the distal end of the shaft of a right femur, with the anterior surface somewhat damaged.

7. Part of the proximal end of a right femoral shaft, with part of the lesser trochanter.

8. A fragment from the proximal end of a left femoral shaft.

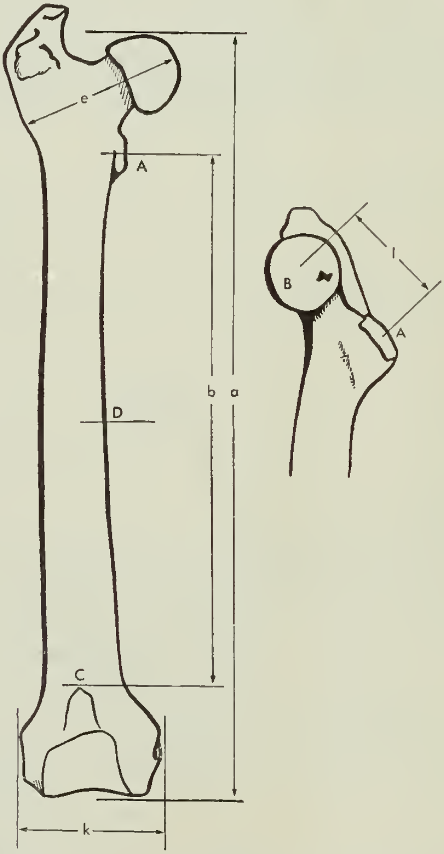


Fig. 9. Anterior aspect of femur, showing dimensions quoted in Table 9. A. Midpoint of surface of lesser trochanter. B. Midpoint of head of femur. C. Transverse plane at proximal margin of shallow pit lying beneath quadriceps tendon. D. Transverse plane midway between A and C.

Dimensions are shown in Table 9. All but the distal extremity and the tip of the greater trochanter is present in one or more of the specimens.

TABLE 9

Dimensions of femur in *Simopithecus* and representative specimens of extant species

a., b., e. See Fig. 9

c. Maximum diameter of femoral head
d. Maximum diameter of femoral neck
f. Maximum diameter of shaft through lesser trochanter
g. Transverse diameter at D (Fig. 9)
h. Antero-posterior diameter at D (Fig. 9)
i. Transverse diameter at C (Fig. 9)

Site/Species and Specimen No.	No. in descriptive list	Known or (probable) sex	Dimensions (see Fig. 9)								
			a.	b.	c.	d.	e.	f.	g.	h.	i.
Kanjera											
M 18807	1	(M)	—	—	27	22	53	—	—	—	—
M 18710	2	(F)	—	—	—	—	—	29·5	—	—	—
M 18909	3	(M)	—	—	—	33·5	—	—	—	—	—
M 11548	4	(F)	—	134·5	—	—	—	29·5	15·5	16	22
M 18708	5	(F)	—	135	—	—	—	30	16·5	18	22
	6	(M)	—	—	—	—	—	—	21*	18*	—
	7	(F)	—	—	—	—	—	30	—	—	—
Olorgesailie											
MS 3991	1	(F)	232	—	—	19	61	—	20	23	—
1731	2	(M)	—	—	35	26	78	—	26	29	—
	3	(M)	—	—	33·5	26·5	77	40·5	—	—	—
	4	(M)	—	—	—	—	—	45	—	—	—
	6	(M)	—	—	—	—	—	(39)	—	—	—
Olduvai											
BK II 693	1	?	—	—	28	21	56·5	30	—	—	—
SHK II E 1203	2	?	—	—	29	25	58·5	—	—	—	—
BK II E 1383	3	?	—	—	—	—	—	—	—	—	28
	4	?	—	—	—	—	—	—	—	—	28·5
T. gelada											
U. Primatol.	—	M	209	140	21	14	44	27	15·5	16	19·5
AMNH 60568	—	M	214	145	21	15	43	27·5	15	14·5	19
P. anubis											
AMNH 82097	—	M	259	183	25	18	54	29	16·5	18	22
AMNH 82096	—	F	232	164	22·5	16	45	24	15	16	21·5
Pan											
USNM 176230	—	M	327	232	37	27	77	40	25	23	36
USNM 176227	—	F	284	194	31	20	67	34	23	21	28
Gorilla											
USNM 239883	—	M	385	240	54	39	110	63	43	36	65
USNM 220060	—	F	299	196	36	23	80	37	27	23	39

* Correct position estimated

The neck is rather short and broad, resembling the condition in *Mandrillus* and *Papio* rather than *Theropithecus gelada*, but the feature is variable. The shaft shows rather strong anterior convexity in all specimens, resembling *Theropithecus* rather than the other living Cercopithecinae, and the muscular impressions, especially the branch of the linea aspera upon which the adductor musculature inserts, are strong.

From their size, Nos 1, 3 and 6 are from male individuals, 2, 4 and 5 from females. The unbroken length of the female femur can be estimated from the two almost complete shafts, Nos 4 and 5, using the formula: overall length/length from mid-point of lesser trochanter to level of proximal margin of sub-quadriceps pit, and substituting the value obtained on the gelada femur. The unbroken lengths of Nos 4 and 5, estimated in this way, are both 201 mm.

The length of the male specimens cannot be directly estimated. However, the breadth through the lesser trochanter of male No. 3 is 112·6% of the mean of female values for this dimension; if its length when unbroken was proportional to this, it was about 226 mm. Fragments Nos 1 and 6 probably came from slightly larger animals; estimates of their unbroken lengths (assuming that their breadth dimensions preserved the same ratios one to another as observed in *Theropithecus*, and that the ratio of length to breadth dimensions was as in female *Simopithecus*), are 234 mm and 231 mm respectively.

Three fragments of the *tibia* are preserved: two distal extremities (M 18718, M 18719) and part of the proximal end. The latter is unregistered.

The two distal ends show the usual cercopithecine features, including the distinct grooves crossing the posterior surface which in life accommodate the tendons of the long digital flexors and M. tibialis posterior. The pit on the lateral surface, representing the position of the inferior tibio-fibular joint, bounded by the rugose area to which the tibio-fibular ligament was attached, is clearly visible. The fragment of the proximal end shows no remarkable features, apart from a prominent rugosity, running antero-proximally, immediately distal to the supposed epiphyseal surface. If the interpretation of the topography of the fragment is correct, this rugosity is too proximally situated to represent the site of attachment of the medial collateral ligament, and must be regarded as pathological. Dimensions of the tibial fragments are shown in Table 10. None of the fragments is sufficiently large to permit the unbroken length of the bone to be reconstructed.

Both the rather small fragments, representing the distal end of the *fibular* shaft, are unregistered. They show no features to distinguish them from modern Cercopithecinae. In one of them, the area of the attachment of the tibio-fibular ligament on the medial surface, and a small part of the tibio-fibular articular facet, can be distinguished.

The tarsus is represented by an associated *calcaneus*, *talus* and *cuboid* (M 18806, M 11549, M 18805) (Plate 13). The talus and calcaneus show no features to distinguish them from corresponding bones in living Cercopithecoidea of similar size. The cuboid resembles that of *T. gelada* in that its lateral border is markedly shorter than its medial, giving it a wedge-shaped outline from the dorsal aspect.

Table 10

Dimensions of tibia in *Simopithecus* and representative specimens of extant species

a. Maximum antero-posterior diameter of distal end
b. Maximum transverse diameter of distal end
c. Ant.-Post. diameter immediately below most distal point of proximal epiphysis
d. Breadth of articular surface of medial condyle, to tip of intercondylar eminence
e. Minimum antero-posterior diameter
f. Maximum length of diaphysis
g. Overall length

Site/Species and Specimen No.	No. in descriptive list	Known or (probable) sex	Dimensions						
			a.	b.	c.	d.	e.	f.	g.
Kanjera									
M 18718	—	?	21·5	29	—	—	—	—	—
M 18719	—	?	23	—	—	—	—	—	—
Unregistered	—	?	—	—	(32)	—	—	—	—
Olorgesailie		?	—	—	—	—	—	—	—
	1	?	—	—	—	20	—	—	—
	2	?	—	—	—	—	17·5	—	—
3723	4	?	—	—	(33)	—	16·5	135	—
3966	5	?	—	—	—	—	(21)	—	—
2108	6	?	—	31	—	—	—	—	—
T. gelada									
U. Primat.	—	M	19	24·5	23	15·5	13	(189)	214
AM 60568	—	M	19	24	24	16·5	13·5	(188)	218
P. anubis									
AMNH 82097	—	M	22	26·5	—	17	16	—	230
AMNH 82096	—	F	18·5	22	—	15·5	13	—	200·5
Pan									
USNM 176230	—	M	29	41	33	26	18	—	275
USNM 176227	—	F	25	36	28	26	19	—	238
Gorilla									
USNM 239883	—	M	40	65	48	38	26	—	307
USNM 220060	—	F	27	42	33	27	18	—	239

B OLORGESAILIE

The deposits at Olorgesailie, Kenya, were described by Leakey (1946) and by Isaac (1966a and 1966b), who summarized the results of his own and previous research. They consist of a series of volcanic ashes, tuffs and reworked sands and gravels of volcanic origin, laid down in the beds of swamps and sluggish, seasonal streams occupying a basin of tectonic origin. The *Simopithecus* remains were virtually all derived from a presumed Acheulian camp and butchering site, DE 89 (Isaac, 1966b), situated on Land Surface 7 of Leakey (Cole, 1954, p. 144). They represent the remains of human meals.

The *Simopithecus* specimens are less well-preserved than those from Kanjera. The nature of the deposit was evidently less favourable for fossilisation, since the surface of many specimens is eroded and friable, with surface detail hard to distinguish. Most of the long-bones were thoroughly cracked and broken, presumably by humans and scavenging carnivores. In addition, most of the individuals represented here were juvenile, so that many epiphyses have been lost. In other respects the material is excellent, specially in the richness of representation of the smaller bones of the extremities, and the almost mint condition of many of the teeth, not a few of which were unerupted crown-germs.

Skull

Useful skull fragments are comparatively rare in the Olorgesailie collection. All are hitherto undescribed.

a. KNM–OG 1421. A fragment of the right temporal, including the glenoid articular area and the zygomatic root. The fragment resembles the corresponding part of the Kanjera female specimen, M 14936, as far as can be seen, but is larger.

b. KNM–OG 1450. The anterior part of a frontal, with the interorbital region presented, but the supraorbital tori absent. The prominent temporal lines curve strongly towards the midline, and obviously came very close to meeting, or actually met, on the frontal bone itself.

c. KNM–OG 1451, 1452, 1453. Three half-frontals, one right, two left, all broken longitudinally exactly in the midline, suggesting that a line of weakness existed in the immature skull along the line of the metopic suture. In the two specimens where this region is preserved, the coronal suture was evidently open at the time of death. In all cases the temporal lines are strongly curved towards the midline.

d. KNM–OG 0001. Part of a juvenile, male, right maxilla, with the series P^3–M^2; a deep concavity on the broken anterior surface represents the alveolus, or perhaps the crypt of the canine, and enables the sex of the individual to be established. M^1 shows slight-moderate wear, with the central dentine 'bridge' just open; M^2 shows slight wear; P^4 shows slight, and P^3 very slight attrition.

The shape of the specimen, so far as can be seen, resembles that of the Kanjera male specimen. With the occlusal plane horizontal, the root of the zygomatic arch lies over the second molar.

e. KNM–OG 0004. Part of the region of the symphysis and right mandibular corpus of an adult male individual. Almost the entire internal face of the right corpus is preserved; the external face is broken away posterior to the position of the fourth premolar. The broken stump of the right canine, and the two right premolars are present. The region of the symphysis is broken obliquely just to the left of the midline, so that the alveolus of the left canine is opened, and the posterior surfaces of the incisor sockets are visible.

The specimen is rather massive. The inferior surface is flat and triangular in shape, as in the Kanjera *Simopithecus*. The canines are stout, and set obliquely, so that their sockets converge inferiorly. The anterior part of the symphyseal surface, between the canines, is extremely narrow, again as in the Kanjera specimens, implying a reduction in the breadth of the incisor series. On the internal surface of the symphysis the usual two shelves are present; the superior one extends posteriorly to the level of the posterior margin of P_3, the inferior to the level of the intercusp clefts of M_1. No trace of a mandibular fossa is apparent on the part of the external surface that is preserved. Behind the narrow incisal region, the corpora diverge markedly, giving a distinctly V-shaped outline to the jaw when viewed from above.

f. KNM–OG 0002. 'Site 10, Bed B, Tr. Fr.' (Plate 18a).

An almost complete right mandibular corpus of a young adult female, with all the premolars and molars present. The specimen is broken anterior to the premolars, but the alveolus of the canine and a small part of the root of the lateral incisor are preserved. The teeth are somewhat damaged, and the chin region is absent. The symphysis is broken just to the right of the midline, but the profile of the two shelves is visible.

The premolars show only slight wear; there is moderate wear on the first and second molars, while the third is newly erupted and shows very slight wear only on the tips of the anterior pair of cusps. A very shallow mandibular fossa, elongated and situated immediately above the inferior margin of the corpus is present. The superior of the two symphyseal shelves extends posteriorly as far as the middle of the fourth premolar; the inferior to the level of the anterior cusps of the first molar.

g. KNM–OG 0003. Part of the right mandibular corpus of a juvenile male, broken at the symphysis. The surfaces of the specimen are badly eroded. The first and second permanent molars are present, M_1 somewhat damaged at its antero-lingual corners. P_4 had not started to erupt at the time of death, but the germ of the crown, in its crypt, has been exposed by breakage. M_2 is only slightly worn; M_1 shows slight-moderate wear, with the central dentine 'bridge' just open. Little morphological detail is visible, apart from the fact that the surface flares outwards in the region of the root of the canine, thus producing a shallow mandibular fossa posterior to this.

h. KNM–OG 0781. Part of the left corpus mandibulae of a juvenile male, slightly younger than the last at death, extending from the level of the canine to that of M_2. At the time of death, the tip of the canine was just about to penetrate the alveolus; it has been exposed by breakage. P_3, the crown of which has also been exposed by breakage since fossilisation, was also unerupted, lying close behind the canine. P_4 is entirely invisible. M_1 was fully in occlusion at death, and shows light-moderate wear. M_2 had emerged from its bony crypt. The specimen agrees in morphology with the previous one.

i. KNM–OG 0005. A fragment of the left mandibular corpus of a young adult male individual, with P_3–M_1. The surface of the mandible is somewhat eroded, and the inferior border is absent. The first molar shows moderate wear, but both premolars are unworn.

Teeth

The structure of the molars and premolars, which are all well-represented, mostly by unworn and unerupted as well as slightly worn specimens, closely resembles that seen in the Kanjera baboon. They are, however, consistently larger (Table 4, Fig. 10) and show a distinct tendency to the development of extra vertical grooves. The male P_3 differs from that of the Kanjera form by the relative shortness of its 'sectorial' face. The male and female canines are essentially the same as those of the Kanjera baboon, but the male teeth, to judge from the unerupted crowns, were even lower-crowned, relative to the general size of the dentition, than in that form. The incisors are represented by an extensive collection in which permanent and deciduous teeth of both sexes must be present. All are small and slender teeth. There are no specimens resembling the broad median upper incisors of *Papio*, *Mandrillus*, and *Macaca*. The small inter-canine breadth in KNM–OG 0004 confirms that the incisors were small. Many deciduous teeth were present in the collection, but were not examined in detail for the present study.

Forelimb

The *scapula* is represented by four fragments, all rather small. (KNM–OG 1454, 1456, 1457, 1458). All are from the distal end, and include the glenoid fossa and part of the neck. In two specimens a small part of the root of the scapular spine is preserved, and this appears to be closer to the surface of the glenoid cavity than in either the modern or Kanjera series. The glenoid cavity itself may be rather shallower than in the Kanjera and modern specimens, but this appearance may be due to erosion of the articular surface in the Olorgesailie fragments.

The *humerus* is represented by seven specimens.

1. 2993. An immature left humerus, complete apart from the proximal epiphysis and some erosion of the distal extremity.

2–3. Two proximal epiphyses.

4, 5 & 6. KNM–OG 1455, 1459, 1460 (FU 1–3/UL). Three fragmentary distal extremities.

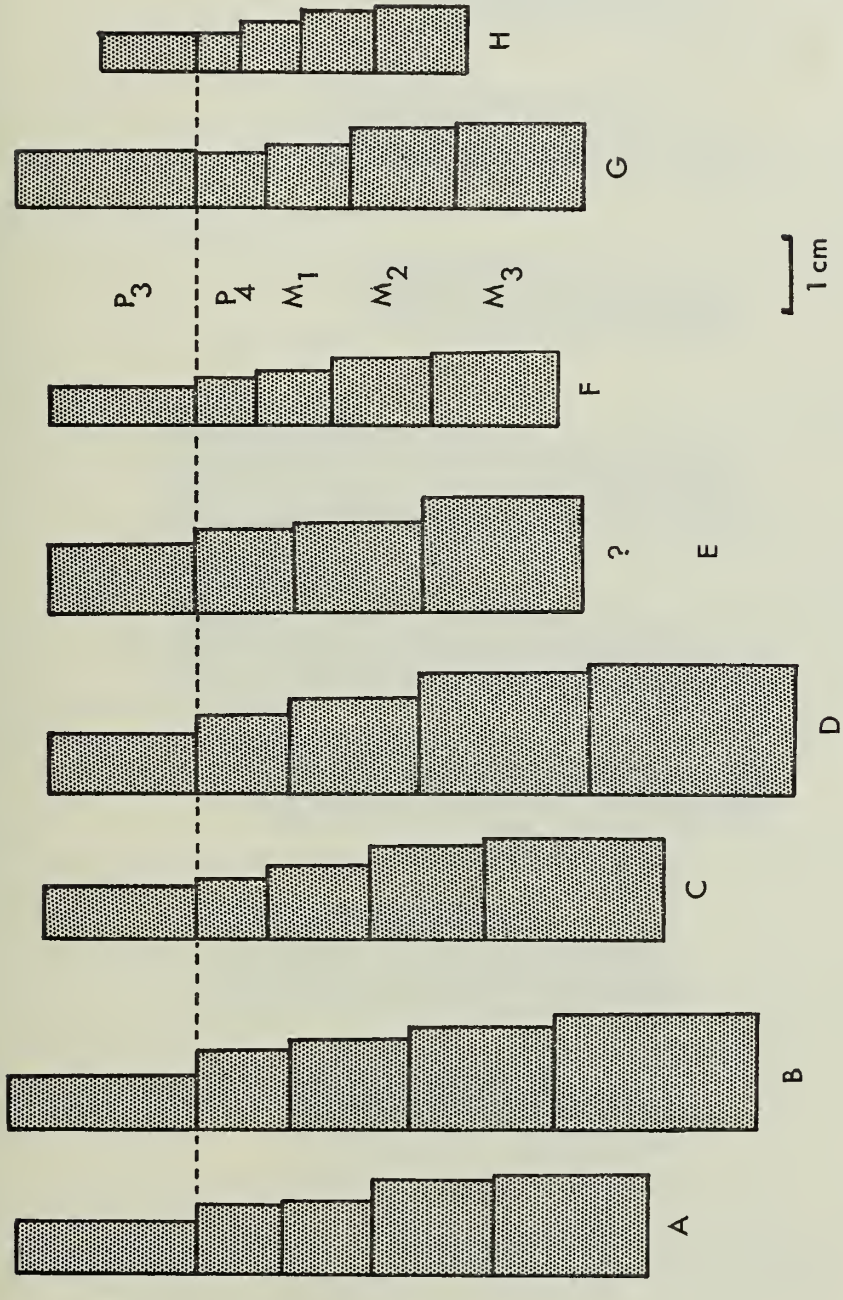
7. KNM–OG 1461. The distal end of a right humerus, with part of the shaft.

In both proximal epiphyses the articular surface appears to be rather flatter than in the modern series or the Kanjera specimen. The distal extremities show the usual cercopithecoid features such as a deep anconeal fossa (probably perforate in life in FU 2/UL). Where the ulnar epicondyle is preserved it is clearly turned backwards as in the modern terrestrial monkeys, but none of the specimens is sufficiently well-preserved for the index of articular breadth to be calculated. None of the specimens with part of the shaft preserved has a prominent brachioradialis flange, and the almost complete specimen shows the straight shaft typical of baboons.

No. 1 is probably from a subadult male individual; 4, 5 and 6 are either from females or from younger juveniles.

The overall length of a male humerus can be estimated by comparing the position of the insertion of the tendon of M. teres major in No. 1 and in male geladas, at a value between 285 and 295 mm. The most complete of the smaller specimens, possibly representing an adult female (No. 5) has a distal articular surface 36 mm in

Fig. 10. Size and proportions of lower cheekteeth in *Theropithecus* and *Papio* males. Sides of rectangles represent length and (anterior) breadth of tooth. a. *T. darti darti* (Makapan). b. *T. darti danieli* (Swartkrans). c. *T. oswaldi oswaldi* (Kanjera). d. *T. oswaldi mariae* (Olorgesailie). e. *T. oswaldi leakeyi* (Olduvai IV) (M_3 unknown). f. *T. gelada*. g. *Papio ursinus* (N = 30, Freedman, 1957) (Largest extant *Papio*). h. *P. cynocephalus kindae* (N = 7) (Smallest extant *Papio*).


A
B
C
D
E
?
F
G
H
P3
P4
M1
M2
M3
1 cm

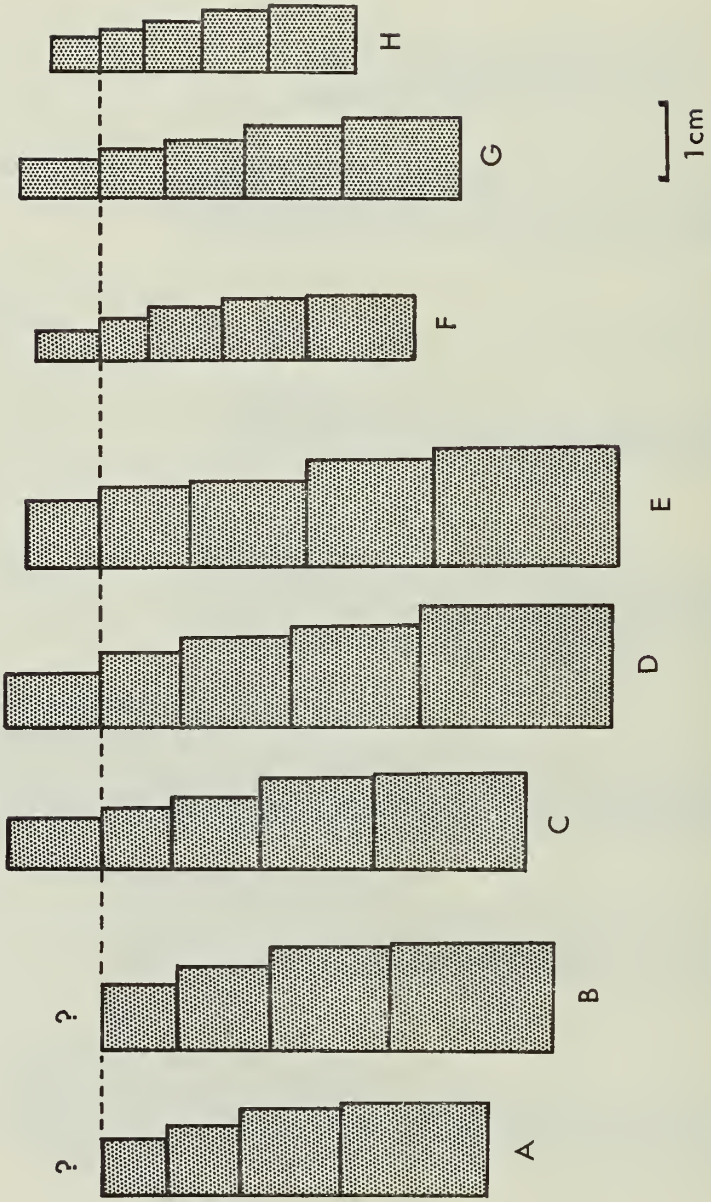


Fig. 11. Size and proportions of lower cheekteeth in *Theropithecus* and *Papio* females. Sides of rectangles represent mean length and (anterior) breadth of tooth. a. *T. darti darti* (Makapan). b. *T. darti danieli* (Swartkrans). c. *T. oswaldi oswaldi* (Kanjera). d. *T. oswaldi mariae* (Olorgesailie). e. *T. oswaldi leakeyi* (Olduvai IV). f. *T. gelada*. g. *Papio ursinus* (N = 7, Freedman, 1957). h. *P. cynocephalus kindae* (N = 17).

breadth; if its overall length was in proportion, this would have been 235 to 245 mm, judging from the relationship between these two dimensions in the male specimen.

Seven fragments of *radii* are preserved: two isolated proximal epiphyses; three more proximal ends, two lacking the epiphyses (OG–1463, 1465, 1466); part of a large but immature radial shaft (OG–1464) and the distal end of a left radius, including the fused epiphysis and part of the shaft (OG–1462).

None of the specimens shows any features to distinguish it morphologically from those of other cercopithecoids such as *Mandrillus, Theropithecus gelada, Papio* and the Kanjera *Simopithecus*. In the immature specimens the volar surface is less deeply excavated. The lateral curvature of the last specimen listed was probably rather less than that of the Kanjera specimen (M 11544) resembling *Theropithecus gelada*.

No estimate of the unbroken length of the mature bone can be obtained from these fragments.

The *ulna* is represented by four specimens, KNM–OG 1467, 1468. Between them they include the complete proximal extremity and about three-fifths of the shaft. All of them show features resembling *Papio, Theropithecus gelada* and the Kanjera *Simopithecus*.

The radial articular facet (three specimens) is deep-set, and the articular surfaces of the anconeal and coronoid processes face largely in a medial direction. The olecranon process is sufficiently well preserved in two specimens for its inclination to the shaft to be apparent, although it is not possible to measure the angle of inclination exactly because the region of the sigmoid notch is damaged and the shaft incomplete. However it is clear that the olecranon was very strongly reflexed, even more extremely than in most individuals of living baboon genera.

Both the *carpus* and the *metacarpus* are well-represented in the Olorgesailie series. It is hoped to make their description the subject of a future publication.

Hindlimb

Eleven separate specimens are present in the collection which can be attributed to the *femur*.

1. KNM–OG 1088 (MS 3991). An adult, right femur, complete apart from some erosion of the surface.
2. KNM–OG 1090 (1731). The proximal end of a right femur, with part of the shaft, the posterior surface of the head, and the greater trochanter slightly eroded.
3. The proximal end and part of the shaft of a right femur, rather distorted and damaged in the region of the greater trochanter.
4. KNM–OG 1470. Part of the proximal end of a left femoral shaft, including the lesser trochanter.
5. KNM–OG 1471. Part of the proximal end of a left femoral shaft, with the surface somewhat eroded.
6. The proximal end and part of the shaft of a left femur, somewhat eroded.
7. The head and neck of a right femur, poorly preserved.

8, 9. Unfused ephiphyses of the femoral head.

10. KNM–OG 1469. The distal end of a femoral shaft, probably left.

11. A fragment of the distal extremity, with one condyle and part of the patellar surface.

The femur of the Olorgesailie *Simopithecus* closely resembles that of the Kanjera form, apart from its greater size. The neck is rather short and broad, the shaft short, stout, strongly marked by muscular attachments, especially those of the adductor group, and showing rather strong anterior convexity. The dimensions of the specimens are shown in Table 9.

Of the specimens upon which meaningful measurements can be taken (1, 2, 3, 4, 6), No. 1 is probably female; the rest are larger and probably male. The overall length of No. 1 is 232 mm. The breadth of No. 2, along the axis of the neck, is 127·9% of the same dimension in No. 1. (No. 3 is closely similar to it). If the length dimension was proportional to this, it was about 297 mm.

The *tibia* is represented by six specimens (KNM–OG 1472, 1473). The most complete of these is an immature right tibia entire apart from the epiphyses. A further specimen, of the left side, has a complete distal extremity. The remaining four are parts of the shaft. At least one is from an immature individual, showing the distal ephiphyseal surface.

The tibia is relatively short-shafted with massive extremities. As in other Cercopithecoidea the shaft has slight convexity towards the lateral side, and is transversely flattened, but does not have a sharp anterior border.

Being immature, the specimens do not show prominent muscular marking. In two specimens, however, an elongated muscle-scar can be seen, immediately medial to the line of the interosseous membrane, which probably represents the area of the origin of M. tibialis posterior.

The dimensions of the tibial fragments are shown in Table 10. None is sufficiently complete to permit reconstruction of the adult, unbroken length.

The *tarsus* is represented in the Olorgesailie collection by several specimens of each bone. Of these, the first and second cuneiformes and the cuboid are of particular interest from the point of view of the locomotory adaptations of *Simopithecus*.

One of the five specimens of *Cuneiform I* (KNM–OG 1474, 1475, 1476, 1477, 1478) is rather larger than the rest, but all have a similar shape and disposition of the articular facets. From the medial aspect, the most striking feature is the relatively small size of the projection of the distal articular surface superior to the body of the bone (the 'beak') indicating that the hallux was relatively small. In this feature *Simopithecus* is even more extreme than any of the modern terrestrial genera.

In a number of specimens the articular surface for the base of the hallucal metatarsal can be clearly seen; it resembles that of *Theropithecus gelada* closely in shape, appearing vertical rather than medially convex from the distal aspect, and with very little expansion on to the medial face of the bone.

From the medial aspect, the inferior margin of all five specimens is evenly convex, unlike any individual of the comparative series of modern genera.

The lateral aspect of the first cuneiform bears the same arrangement of articular facets for the second cuneiform and the base of the second metatarsal as in living cercopithecoids. The two facets on the 'beak' are relatively much smaller than those of the modern arboreal and semi-arboreal genera, and also than *Papio*, agreeing in relative size with those of *Theropithecus gelada*.

Cuneiform II is represented by three specimens. One of these, from the left side (KNM–OG 1479), is intact apart from some damage in the region of the tuberosity, and the details of the articular surfaces can be clearly distinguished.

The distal surface is deep relative to its breadth, and is approximately symmetrical about its long axis, the condition also seen in *Theropithecus gelada*, among modern genera. In those forms which have a larger hallucal metatarsal, and hence a more extensive 'beak' on the first cuneiform, the medial margin of the proximal face of the second cuneiform is much longer than the lateral, in order to support the large 'beak'. The morphology of the lateral surface shows no remarkable features, but that of the medial surface reflects the reduction of the 'beak' of the first cuneiform in the relatively very small size of the anterior articular facet; this is much less in anterior-posterior diameter than the interval separating it from the posterior facet (Fig. 12).

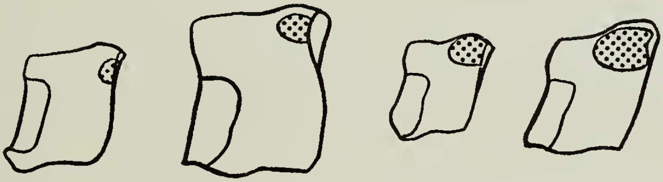


FIG. 12. Medial aspect of right cuneiform II. Left to right: *T. gelada*, *T. oswaldi mariae*, (Olorgesailie), *Cercocebus atys*, *Mandrillus leucophaeus*. Note variation in relative size of facet for 'beak' of cuneiform I (Stippled)

Two specimens of the *cuboid* are present in the collection, both somewhat damaged, but between them representing the whole bone (KNM–OG 1480, 1481). Both are clearly of the highly asymmetrical shape seen in *Theropithecus gelada*, with the medial face very much less extensive than the lateral. A distinct facet for the sesamoid of M. peroneus longus is present, but this is small relative to the size of the bone.

The *metatarsus* is represented by a number of specimens, of which the following are complete enough to be of descriptive value.

The *first metatarsal* is represented by a single, complete and evidently mature specimen in which the epiphyses are fused (KNM–OG 1482). It is of the left side. The head resembles that of *Theropithecus gelada* rather closely; there are no large, projecting flanges on either side of the articular surface such as are found in *Papio*, *Mandrillus* and the arboreal genera, and which in these forms support the large sesamoids of the long hallucal flexor. The fossil also resembles the gelada in having the head inclined slightly but distinctly medially. The functional significance of this feature is obscure. The base has no large scar marking the area of insertion of the tendon of the M. peroneus longus, again in agreement with *Theropithecus gelada* and contrasting with the condition seen in other, less terrestrial forms, and the proximal articular surface is more vertically elongated, less curved, than in *Papio* and *Mandrillus*, matching the shape of the distal articular surface of the first cuneiform.

In size, the specimen is comparable to that of a modern *Mandrillus*. Its size relative to the rest of the foot cannot be expressed exactly, since it was not associated with any of the remaining metatarsal specimens, most of which represent immature individuals. These specimens are all very much larger than the corresponding bones in the mandrill, however, suggesting that the first metatarsal was in fact relatively small in the fossil form. This fact may be quantified by expressing the length of the first metatarsal as a percentage of the breadth of the proximal surface of the cuboid, of which two specimens are known from Olorgesailie. Both of these have a breadth of approximately 21 mm giving an index of 229, a very low figure when compared with values obtained for modern genera: *Theropithecus gelada*, 253; *Papio*, 284; *Mandrillus*, 300; *Cercocebus*, 305. It might be argued that an artificially low value obtained for the Olorgesailie form was due to a sex difference between the specimens, the two cuboids representing males, while the first metatarsal was from a female individual. In this case the error could be compensated by multiplying the metatarsal length by 5/4, a reasonable expression of the amount of sexual dimorphism seen in the long-bones of *Simopithecus*. The index derived from the corrected figures is 286, which is close to the value obtained for *Papio*, and still well below that of more arboreal forms. In fact, it is unlikely that the first metatarsal was derived from an individual much smaller than those from which the cuboids came; the size of its proximal articular facet corresponds in size to the distal articular facets of the *largest* first cuneiformes, which are themselves compatible in size with the cuboids.

The *second metatarsal* is represented by two specimens, one of each side, both consisting of the proximal end and the shaft, broken short close to the distal extremity, probably at the epiphyseal line (KNM–OG 1483, 1484). Both are therefore probably from immature animals.

The shaft is very short and stout, and exhibits rather marked lateral convexity. The proximal articular surface is extremely deep and transversely narrow, being most closely approached in this feature by *Theropithecus gelada* among the comparative series. The same surface also resembles that of the terrestrial monkeys in being almost symmetrical about the longitudinal plane of the bone, but the condition is less extreme than in the gelada or in the Olduvai specimens described below, most closely approaching *Papio*. The facets on the lateral side of the base resemble the general condition in living monkeys, but those of the medial side resemble *Theropithecus gelada*, and differ from *Mandrillus* and the arboreal genera, in that the superior facet is subequal to, and not larger than, the inferior.

The *third metatarsal* (KNM–OG 1485, 1486, 1487, 1488) is represented by four specimens, three left and one right; all consist of proximal extremities from which the inferior part is missing, together with a variable amount of the shaft. One specimen, of the left side, extends as far distally as the line of the distal epiphysis. All are probably immature.

Although the full depth of the proximal articular facet is not present, it was obviously extremely narrow and deep. The arrangement of the facets of articulation on the lateral and medial surfaces of the base is as in other cercopithecoids. From the dorsal aspect, the dorsal surface of the base extends proximally in a wedge-shaped process; this is long and acutely pointed, as in *Theropithecus gelada*. The shaft is again very stout, and is marked by strong ligamentous tubercles at the proximal end. The dorsum is flat, and the angulation between it and the sides of the shaft is sharp.

The *fourth metatarsal* is represented by eight fragments, four of each side (KNM–OG 7493, 1494, 1495, 1496, 1497, 1498, 1499, 1500). Most are rather badly damaged, but one has the shaft complete as far as the distal epiphysis.

The shaft is stout, and marked with extraordinarily strong ligamentous impressions. None is sufficiently intact to permit the depth and breadth of the proximal articular surface to be measured accurately, but this was obviously again very narrow and deep. The arrangement of articular facets on the proximal extremity is as in other cercopithecoids.

Four specimens of the *fifth metatarsal* are included in the collection, two from each side (KNM–OG 1489, 1490, 1491, 1492). All consist of proximal extremities, one (of the right side) with the whole of the shaft and part of the head.

The shaft shows moderate medial compression and some medial convexity, but both conditions are less developed than in *Theropithecus gelada*. The shaft is short and stout, also unlike *Theropithecus gelada* in which it is slender, specially relative to those of the other metatarsals.

The facet for the fourth metatarsal is as in other monkeys. The tubercle on the lateral side of the base (for the insertion of M. peroneus brevis) is very massive and

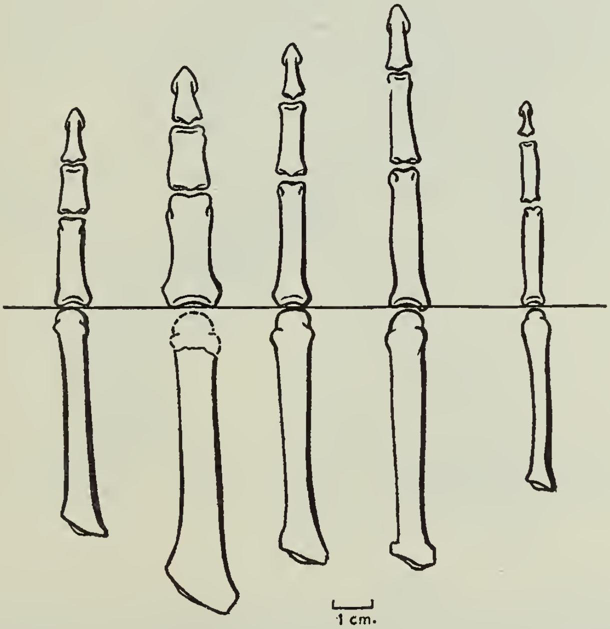


Fig. 13. Third right metartarsal and phalanges, to scale. Left to right: *Theropithecus gelada* male (UPHE); *T. oswaldi mariae*, Olorgesailie (composite); *Papio anubis* (AMNH 82906) male; *Mandrillus sphinx* (AMNH 89364) male. *Cercocebus atys* male.

prominent in all the specimens, resembling the condition seen in *Theropithecus gelada*.

The best preserved of the specimens of metatarsals II–IV, all of the left side and at a similar stage of maturation, probably represent a single foot (KNM–OG 1484, 1485, 1493, 1491). When articulated, they form a very short, broad metatarsus, with a deep proximal articular surface (Fig. 14). Both of the first two features contrast strongly with the elongated, narrow metatarsus of *Theropithecus gelada* and some species of *Papio* (e.g. *P. cynocephalus*), and resemble most closely the more thickset species of the latter genus, such as *P. anubis*, although even these are far less extreme in robusticity than the fossil.

Phalanges are well represented in the Olorgesailie collection (KNM–OG 1501–1520). Unfortunately, as no specimens were associated, and material of many individuals of both sexes is known to be present, there is no means of distinguishing manual from pedal phalanges, or of identifying phalanges of a particular digit (apart from hallux or pollex).

Eleven proximal phalanges are known, of which one is clearly of a first digit, probably the hallux. All are extremely short and stout, exceeding even the gelada in this feature. Specimens sufficiently well-preserved for their relative robusticity to be shown graphically by plotting their length against their basal breadth are shown in Fig. 15. All are quite different from the modern arboreal genera, and exceed even *Theropithecus gelada* in the value of the index.

The middle phalanges, of which nine are known, agree in shape with the proximal, indicating even shorter and stouter digits than are seen in *Papio* and *Theropithecus gelada*. The distal phalanges, represented by four specimens, of which one is probably of the pollex, are of the shape normal in Cercopithecoidea.

C. OLDUVAI, UPPER BED II SERIES

Accounts of the geology and stratigraphy of Olduvai gorge, northern Tanzania, were published by Reck (1926) and Leakey (1951) while the preliminary results of

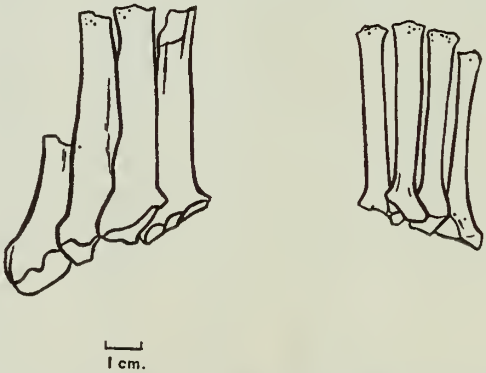


FIG. 14. Articulated juvenile metatarsus, excluding metatarsal I. Left: *Simopithecus* (Olorgesailie). Left foot, diaphyses of all but metatarsal V virtually complete. Right: *Papio* sp., male (UPHE). Right foot. Epiphyses removed. Note close appression of metatarsals of fossil specimen.

more detailed geological surveys have been published by Pickering (1958, 1960, summarized by Bishop, 1963) and Hay (1963, 1967). The latter author summarizes the results of his own and previous studies as follows:

> 'Bed I at Olduvai is a conformable sequence of lava flows and varied sedimentary deposits that extend upward from a welded tuff overlying the Precambrian basement to the top of a widespread marker bed. Bed II is a sequence of lacustrine clays and laterally equivalent fluvial, eolian and pyroclastic deposits. Bed III comprises alluvial deposits and a laterally equivalent assemblage of fluvial, lacustrine and eolian beds. Bed IV can be widely subdivided

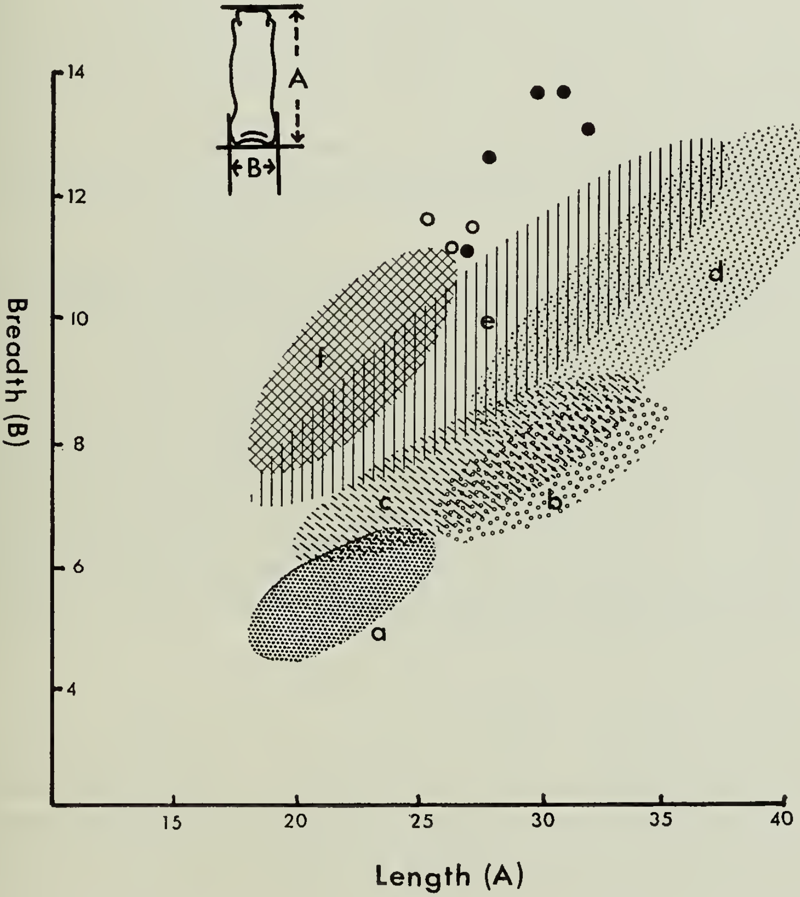


FIG. 15. Basal phalanges of hand and foot; breadth plotted against length, with selected percentiles of index Breadth/Length. Shaded areas represent observed range of phalanx shape in each extant genus. a. *Cercopithecus* (N = 40). b. *Cercocebus* (N = 40). c. *Macaca* (N = 40). d. *Mandrillus* (N = 40). e. *Papio* (N = 80). f. *T. gelada* (N = 40). Open circles: *Simopithecus*, Olduvai. Solid Circles: *Simopithecus*, Olorgesailie.

> into a lower unit of fluvial clays, sandstones and conglomerates and an upper unit of eolian tuffs. Although moister than that of the present day, the climate was relatively dry throughout much of the time that these beds were deposited. Semi-desert or desert conditions rather like those of the present day may have prevailed at least twice. Tectonic movement seems to have taken place between the deposition of Beds III and IV'.

Leakey (1963) emphasises that a stratigraphical, faunal, cultural and probably climatic break exists between the upper and lower parts of Bed II. A series of Potassium/Argon dates for Olduvai material (Leakey, Evernden and Curtis, 1961, Hay, 1963) appear to confirm the existence of this hiatus, and also indicate the very long time span of the Olduvai deposits – greater than $1 \cdot 7 \times 10^6$yrs. Later fieldwork by Hay (1967) indicates that the Bed I–Lower Bed II series is separated from the upper sequence by major tectonic events associated with Rift Valley faulting, which destroyed the permanent saline lake. This was replaced by a 'broad, playa lake and alluvial plain' (Hay, 1967).

As Leakey (1963, 1965) has pointed out, the value of many of the earlier collected specimens is reduced by their being assigned to an incorrect horizon, or none at all. This applies to many of the British Museum specimens which are marked merely 'Olduvai'.

A further complication factor is the presence at Olduvai of at least two other Cercopithecoidea as well as *Simopithecus*; there is a distinct possibility that skull fragments or postcranial bones not directly associated with teeth have been wrongly attributed.

By far the greatest amount of Olduvai *Theropithecus* material is derived from BK II, a site in the latest layers of Bed II fossiliferous deposit that consists of the clay infilling of a former stream-channel (M. D. Leakey, 1967). It includes cranial, dental and postcranial material, mainly in a fine state of preservation, though somewhat fragmentary. A second, smaller, series consisting of well preserved postcranial bones, is derived from site SHK II, which is believed to be of a broadly similar, but slightly earlier, age (M. D. Leakey, 1967). Although its attribution to *Theropithecus* must be provisional until confirmed by associated cranial or dental material, it is close in structure and size to the BK II series.

Skull

a. M 18772, BK II 9.V.35. (Plate 14a)

A frontal, complete apart from the extreme lateral part of each side. The posterior surface of the fragment, at least in the region of the bregma, corresponds exactly with the line of the coronal suture. The temporal lines are sharp and prominent, and are situated far up on the superior surface of the frontal. The supraorbital torus is rather heavy and rounded, and divided in the centre by a shallow depression.

b. BK II 1957 (Plate 17a)

A skull, probably female, almost complete apart from the facial region and the mandible. No apparent post-mortem distortion.

Death was probably due to injuries associated with a depressed fracture of the right parietal and frontal region. The depressed area is bounded anteriorly by a semi-circular fracture of the bone, but posteriorly by a flexure of the bone which must have occurred when this was in a fresh condition. A pair of parallel, shallow grooves runs antero-posteriorly across the depressed section of bone. If, as seems likely, the injury was caused ante or ad mortem by a blow from a missile or hand-held weapon, this blow probably fell from the right side.

In general shape, the braincase resembles that of the Kanjera *Simopithecus*: its profile between the glabella and inion is rather flatter than that seen in *Theropithecus gelada* and resembles the condition in *Papio*. The temporal lines, which appear to be single, are raised and come close to meeting about the bregma, but then run parallel to about one centimetre from the inion, where they begin to diverge, finally intersecting the nuchal line about a centimetre each side of the inion. In the region where the two lines are close together there is marked keeling of the cranial vault. The supra-orbital tori resemble those of the Kanjera specimens in shape, rather thick and shelf-like, and divided by a shallow rounded depression. The supra-orbital notches are deep. The orbits themselves are incomplete, the specimen being broken across the nasals and at the zygomatico-frontal suture. The roof of the right orbit, and part of the left, are preserved, and it can be seen that the optic foramen resembles that of modern cercopithecines.

The inion is prominent, and higher than the adjacent occipital crests, which widen laterally to become confluent with the temporal end of the zygomatic arches. There is scarcely any lateral projection of the mastoid processes beyond the line of the occipital crests, as in the Kanjera *Simopithecus* and *Papio*, but unlike the gelada in which the mastoids are strongly laterally-projecting. The nuchal region of the occipital bone is closely similar to that of *Theropithecus gelada* in shape; that of *Papio* (and still more that of *Mandrillus*) is more acutely angled posteriorly when viewed from the basal aspect. This may be related to the posterior disposition of the main mass of the fibres of the temporal muscle in these forms. The foramen magnum and the occipital condyles present no unusual features.

The whole of the base of the skull anterior to the foramen magnum is broad relative to its length. This shape is reflected in the width of the basilar part of the occipital. The pair of fossae situated on its external surface to either side of the midline, which may be associated with the areas of insertion of the Mm. longus and rectus capitis, are more extensive than in living genera, occupying most of the basal surface. This feature may be related to the shortness of the skull-base, but also perhaps to an unusually large development of the muscles concerned. The basal suture was open at the time of death.

The petrous and tympanic parts of the temporal are somewhat damaged, but their general appearance is as in *Papio* and *Theropithecus gelada*. The external auditory meatus faces more directly laterally, and less posteriorly and superiorly, than in modern *Papio*, but the feature is less marked than in the Kanjera male.

The articular region is shaped much as in the living genera, and is without the distinct laterally-facing surface seen in the Kanjera male. The post-glenoid tubercle is long and massive, and as in the Kanjera male, it is in close contact with the external auditory meatus, reflecting again the shortness of the skull-base, a feature directly opposed to the condition in forms of *Papio* and *Mandrillus* of comparable size.

Only the posterior parts of the pterygoid fossae are preserved, and of these only the right has been developed from the matrix. The characteristic line running up the medial surface of the lateral pterygoid plate, as in the Kanjera specimen, can be distinguished.

c. BK II (Plate 15a and b)

An almost complete juvenile female corpus mandibulae (figured in Leakey and Whitworth, 1958, as *S. oswaldi*). On the left side the incisors, canine, premolars and first two molars are fully erupted and in occlusion. The third molar had not started to break through the alveolar bone at the time of death, but owing to post-mortem damage is visible in its crypt. On the right side, the incisors, canine, premolars and first two molars are present and in occlusion. The jaw is broken short immediately posterior to the second molar, but the anterior and inferior surfaces of the crypt of M_3 are present. The specimen is somewhat cracked and probably slightly expanded by matrix-filled cracks. A slight asymmetry of the two halves suggests that some post-mortem distortion has occurred.

The incisors show moderate wear with their tips worn to a flat surface; the canines show only very slight wear. The third premolars are unworn apart from an extremely small wear-facet on the tip of the higher cusp of each. The fourth premolars have small wear-facets on both cusps. M_1 is moderately heavily worn, with a single area of dentine exposed over its whole surface. The second molars are unworn, apart from a small wear facet on the anterior buccal, and an extremely small facet on the posterior buccal cusp. The age of the individual at death was therefore probably rather greater than that of the Kanjera juvenile female (F 3398).

The jaw is rather broader and more massive than that of the Kanjera individual, and the superior symphyseal shelf is relatively longer, extending backwards, when the jaw is held with the occlusal plane horizontal, to the level of the posterior half of P_4. The inferior symphyseal ('simian') shelf has much the same extent as in F 3398, reaching to the anterior cusps of M_1. No mandibular fossa is present. The inferior surface of the symphyseal region is flat and triangular. Two mental foramina are visible on the left side, beneath the anterior part of P_4.

d. Old. BK II Ex. 1953/117

A fragment of the posterior end of the left side of a mandibular corpus, with M_2 and the roots, broken short, of M_3. M_2 shows moderate wear; M_3 was perhaps not fully erupted at the time of death.

e. M 14953 BK II Red bed (Plate 15c and d)

Mentioned by Hopwood, (1936). Illustrated (as male) by Leakey and Whitworth. The left side of a corpus mandibulae, with the three molars and P_4 present and reasonably well-preserved. P_3 is represented only by the posterior part of the tooth and its root. The impression of the anterior root of P_3 is however visible on the surface of the broken alveolus; from the size of this it seems likely that the individual was female, rather than male as stated by Leakey and Whitworth. The corpus itself is badly cracked and distorted, but the position of the superior symphseal shelf is determinable; this extends posteriorly as far as the posterior part of P_4. The third molar is newly erupted, showing wear on its anterior lingual cusp only. M_2 and P_4 are moderately worn, while M_1 is heavily worn.

f. M. 18779 (Plate 14d and e)

(This specimen is tentatively included with the Upper Bed II series. The label enclosed with it stated that it comes from Broken Hill; however, no non-human primate cranial material is known from this site (Leakey 1956). It bears the inscription 'Old-y II' and is hard and black, quite different from the friable, pinkish-red Broken Hill postcranial bones (M 18776, M 18777, M 18778).)

A fragment of a right maxilla, female, with the canine and two premolars *in situ*. The anterior margin of the fragment is probably the maxillary-premaxillary suture. A moderately large wear-facet is present on the posterior face of the canine; the premolars are scarcely worn, with the dentine exposed only at the tips of the cusps. The buccal root of P^4 was probably exposed on the maxillary surface before death.

As in specimens from Kanjera there is a complete absence of maxillary fossae.

g. M 14681 (Plate 14b and c)

Described by Hopwood (1934) as *S. leakeyi*. This specimen is also tentatively referred to the Upper Bed II form. Part of a left maxilla with M^2 and M^3 in position, the alveoli of M^1–P^4 and part of the posterior wall of the canine socket preserved. The small size of the canine indicates a female individual. M^2 shows moderate, and M^3 slight to moderate wear. The buccal roots of the second molar were probably slightly exposed. The posterior palatine foramen is at the level of the posterior cusps of the third molar, and situated close to the base of the alveolar eminence. With the occlusal surface horizontal, the root of the zygoma is above the anterior cusps of M^3.

Teeth

The teeth of the Bed II *Theropithecus* agree with those of Kanjera and Olorgesailie in general structure. The distinctive pattern of grooves clefts, and fossae is well developed in the cheek-teeth, while the upper and lower canines of the females are relatively small. The small size of the incisors is well documented by the juvenile female mandible, 'c' in the descriptive list. No male anterior teeth were available for study.

In size, those few teeth which can be readily sexed are comparable to the low end of the Olorgesailie range.

Postcranial Material

As mentioned, at least two cercopithecoids apart from *Theropithecus* occur at Olduvai. All specimens which could not be excluded from the genus on grounds of size or morphology are described here; some may well be wrongly attributed.

The *humerus* is represented by three specimens.

1. 1384 5K IIE. The complete distal extremity and about three-fifths of the shaft of a left humerus. There is some damage to the anterior surface of the shaft, and very slight erosion of the sharper edges of the distal extremity.

The shape of the specimen is much as described for the Kanjera baboon, but strong spiral grooves, which in living forms are occupied by the M. brachialis, are present. In addition, the brachioradialis crest is rather more prominent than in the Kanjera specimens, though less so than in *Mandrillus* among the modern series.

2. BK II 118

The distal extremity and about three-fifths of the shaft of a left humerus, well-preserved apart from general loss of detail through erosion of the surface, especially of the distal end. Both epicondyles are broken.

The shaft appears exceptionally straight, from both lateral and anterior aspects. The anconeal fossa is perforated, and was probably in this condition in the live animal. The brachialis-brachioradialis crest and flange are low as normally in *Theropithecus*, and no spiral grooves are present.

3. SWK II F 2953

A well-preserved fragment of the distal end of a right humerus. It resembles 1384 BK IIE in morphology, but the spiral grooves are lacking, and the ulnar epicondyle is rather larger and more medially projecting.

The dimensions of all three specimens are included in Table 6. Both specimens (1 and 3) for which the index of relative epicondylar breadth could be calculated had a lower value than was found in the Kanjera *Simopithecus*, and also fell outside the range of modern *Papio* and *Theropithecus gelada*, lying within the range for *Mandrillus* (Fig. 5).

Two specimens may be attributed to the *radius* of *Simopithecus*.

1. Is 1941

A fragment of the proximal end of a left radius. The bicipital tuberosity is prominent and the volar surface rather deeply excavated.

2. BK II 1953/54

The head, neck, and part of the proximal end of the shaft of a left radius. Surface detail is well-preserved. The bicipital tuberosity is distinct. The surface of insertion of the M. supinator is marked off from the volar surface by a strong raised fascial line. Its surface is marked with faint parallel grooves probably representing the positions of the fibres of the supinator. The interosseous margin is prominent, and the volar surface rather deeply excavated.

The *femur* is represented by two proximal and two distal extremities.

1. BK II Surface 693 1953

The complete proximal end of a right femur with only slight damage to the head. The shaft is broken obliquely below the level of the lesser trochanter, so that more of the medial than the lateral surface is preserved. The morphology of the fragment resembles that of Kanjera specimens, having a rather short, broad neck, and massive greater trochanter, the tip of which faces more directly medially than in most living Cercopithecoidea, and almost overhangs the margin of the head. A deep pit, distal to the lesser trochanter on the posterior surface and extending to the broken margin of the fragment, probably represents the origin of the most proximal part of the adductor mass.

2. SHK II E 1203

The proximal end of a right femur, together with part of the posterior surface of the shaft, the anterior surface mainly absent. This specimen resembles the last, except that the muscular markings on the lateral surface of the greater trochanter are stronger, perhaps indicating a rather older individual.

3. BK II E 1383

The distal end of a right femur, with part of the shaft.

4. Olduvai (R)

Distal end and part of the shaft of a left femur.

These two specimens are closely similar in shape and size, and may perhaps be attributed to the same individual. The shape of the shaft and the muscular and tendinous impressions on the distal extremity resemble those of modern Cercopithecoidea. The most remarkable feature of both is the extraordinary orientation of the condyles on the shaft, which leads to a degree of 'kneeing-in' equivalent to that regularly seen in hominid femora. The feature is highly variable among cercopithecoid monkeys, more so, apparently, than among either the Pongidae or the Hominidae; occasional individuals (e.g. a specimen of *Mandrillus* in the collection of the Primatology Unit, Royal Free Hospital) have as much convergence at the knees as is seen in the Olduvai individual.

The dimensions of the femoral specimens are shown in Table 9, p. 41.

No specimens of the leg are known from Olduvai.

The *tarsus* is represented by an associated talus and calcaneus (BK II 63 and 315), and two well-preserved examples of the talus (BK II 1050 and SHK 400). These specimens resemble the corresponding bones of the Kanjera form and are of the shape usual in large, heavily-built quadrupedal monkeys.

Metatarsus and *phalanges* are represented by seven specimens, of which the first four were associated, and are presumably from one individual.

1. BK II 1952 316

The proximal extremity of a second right metatarsal, with part of the shaft, the proximal and lateral surfaces somewhat damaged.

From the proximal aspect, the base appears extremely narrow and deep, more so than any of the modern comparative series, but most closely approached by the gelada. The proximal articular surface resembles that of the modern terrestrial genera, and is quite unlike that of the arboreal and semi-arboreal forms, in being symmetrically T-shaped, indicating little torsion of the second digit in the living animal. The articular facets of the lateral aspect are similar to those of the species in the modern series. The most striking feature of the medial aspect is a prominent tubercle representing the attachment of the interosseous ligament. The articular facet lying postero-dorsal to this, which articulates with a corresponding facet on the 'beak' of the first cuneiform, is relatively small. This agrees with the condition seen in the gelada and Olorgesailie *Simopithecus*, and contrasts with that seen in those (arboreal and semi-arboreal) genera in which a large cuneiform 'beak' supports the massive hallux.

2. BK II 1952 317

The proximal extremity of a right third metatarsal, matching the previous specimen. The styloid process is absent. The bone is marked by strong ligamentous tubercles; the dorsum is flat and the angulations between the dorsal and lateral surfaces sharp, perhaps indicating that the metatarsals were closely appressed in articulation, as in the gelada and the Olorgesailie *Simopithecus*. The wedge-shaped process of the dorsal surface extending proximally is long and acute, again as in the gelada among modern forms, and unlike the condition in arboreal monkeys. The small, convex facet on the medial aspect (for the second metatarsal) and the larger, concave one on the lateral face (for the fourth) are unremarkable.

3. BK II 1952 318

A whole, well-preserved proximal phalanx, attributable to the foot by its association with the previous specimens, and probably of the second digit. All surface detail, including tendinous grooves, the impressions of the attachment of the flexor sheath, and the outlines of joint-surfaces, are very clearly preserved. Dimensions of this specimen have been included in Fig. 15, in which the breadth of the base of proximal phalanges is plotted against their length. With a breadth exceeding 40% of its length, this specimen is approached in stoutness only by *Theropithecus gelada* among modern monkeys, agreeing with the Olorgesailie specimens.

4. BK II 1952 319

A complete, excellently preserved middle phalanx, probably from the second pedal digit. This specimen again exceeds any of the modern series in its shortness and stoutness, which is only approached by the corresponding bone in *T. gelada*. It is quite unlike the long, slender middle phalanges of the more arboreal monkeys.

5. SHK II 286

A third right metatarsal, perfectly preserved apart from a small shaving in the region of the more dorsal of the two facets for metatarsal IV. The specimen is considerably smaller than BK II 1952 317 and so is probably from a female individual.

The most striking feature of the specimen is the relative shortness and stoutness of the shaft, and the relative massiveness of the proximal extremity. In particular, the tendinous markings of the proximal end extend further distally on to the shaft than in modern forms. The proximal articular surface is deep and narrow, and as in BK II 1952 the base extends proximally in a long and acutely wedge-shaped process. The articular surface is flat, rather than convex as in the more arboreal monkeys. The shaft is less strongly angulated than in BK II 1952, resembling the gelada. The morphology of the head region is normal for a cercopithecoid monkey, except that the groove immediately posterior to the articular area on the dorsal surface is exceptionally deep. Such a development of the groove is regular in animals such as those Carnivora which are habitually digitigrade on their hind feet. However, the groove is rather irregular in occurrence among living monkeys, and in them does not appear to be related to posture, so that it would be unwise in the absence of other evidence to infer that the Olduvai *Simopithecus* was habitually digitigrade on its hind feet. The two small facets for the second metatarsal, situated on the medial surface of the base, are separated by a broad, shallow groove, as in other large cercopithecoids. In the smaller monkeys the facets are proportionally larger, and the tendinous groove narrower, a feature probably related to the need for greater tendinous support for the foot in the larger forms. The two facets on the lateral side, for metatarsal IV, resemble those of other monkeys in shape and relative size.

6. BK II 1953/69 and
7. Olduvai (un-numbered)

Two well-preserved proximal phalanges. In the absence of associated material it is not possible to attribute these specimens with certainty to the hand or the foot, but this does not affect the functional implications of their shape; they could only have been derived from a terrestrial form, as can be deduced from their breadth/length ratio, which exceeds 40% in both.

D. Olduvai, Bed I and Lower Bed II Series

Available material antedating the 'faunal break' at Olduvai consisted of two partial mandibles from site DK I, and a damaged talus from HWK. The former is close to the base of the Olduvai sequence, while the latter, formerly believed to lie within Bed I, is now thought to belong to the lower part of Bed II. (M. D. Leakey, 1967).

Skull

a. M 14937 DK I

Part of a right mandibular corpus, with molars and P_4 present. M_1 is very heavily worn, M_2 heavily worn and P_4 and M_3 moderately worn.

b. M 14938 DK I. Mentioned, as *S. leakeyi*, by Hopwood (1936). (Plate 16).

Part of the right corpus mandibulae of an adult female individual, with M_3, P_4, P_3 and the vacant alveoli of the first two molars. The posterior part of the canine root, and the posterior surfaces of the alveoli of the right incisors are also present. The specimen is broken at the symphysis just to the left of the midline, so that the symphysis is shown in cross section. The third molar and the premolars show moderate wear. The superior symphyseal shelf extends posteriorly to the level of the anterior part of P_4, the inferior to the level of the anterior cusps of M_1. The inferior surface of the symphysis is flat. Three mental foramina can be distinguished, about one-third of the distance from the inferior to the alveolar margin, below P_4 and M_1.

The specimen shows several interesting points of difference from the females of the Kanjera, Olduvai II and Olorgesailie forms. There is a distinct, though not deep, mandibular fossa defined superiorly by the flaring alveolar margin below M_1–P_3, and the raised mandibular border in the same region. The mandibular corpus deepens appreciably anteriorly reaching its greatest depth below the mesial cusps of M_1, and the anterior part of the symphyseal shelf is rather more steeply-sloping. In each of these characteristics it is reminiscent of *T. gelada*.

Teeth

All the available teeth of the Bed I baboon are rather badly worn or damaged. The structure of the molars and premolars shows no differences from other populations which could not be attributed to individual variation. (They are somewhat smaller than those of the later, Bed II form).

The bi-incisal breadth in M 14938 can be estimated at about 15 mm, indicating that the incisors showed the reduction in relative and absolute size characteristic of the genus.

Postcranial Material

The single damaged talus from HWK (M 18771) is of the usual form for a large terrestrial cercopithecine.

E. OLDUVAI, BED IV SERIES

Skull

Two mandibular specimens from Bed IV were available.

a. M 14680 Bed IV (Plate 16a and b)

Part of the right side of a juvenile male mandible, described by Hopwood (1934) as the type of *S. leakeyi*. Little is visible of the shape of the mandible, which is very badly cracked. The first molar is fully erupted, and shows light wear. The anterior deciduous premolar is still in position. None of the other permanent cheek-teeth had begun to erupt at the time of death, but the germs of M_2, P_3, P_4 and the canine were fully formed and have been exposed by dissection of the alveolar surface. As in modern genera, the roots of the unerupted P_3 are 'astride' the canine, and both it and P_4 are rotated so that the anterior root is on the buccal side.

b. Old. 1472, 57 Bed? IV, Site JLK; the type of *S. jonathani* Leakey and Whitworth 1958. (Fig. 16)

A mandible, complete apart from some damage to the incisal region. Some post-mortem distortion is shown by the asymmetry of the two halves. The dentition is complete apart from the incisors and the right P_3. All the molars show extreme wear, the first being reduced to little more than stumps. The morphology of the jaw has been described by Leakey and Whitworth (1958). Its most notable features are the massiveness of the corpora, and the relative height of the rami. Leakey and Whitworth draw attention to the more vertical position of the ascending ramus as compared with that of the Kanjera form. In all their illustrations the left side is figured. Owing to post-mortem distortion of the specimen, the ramus of this side

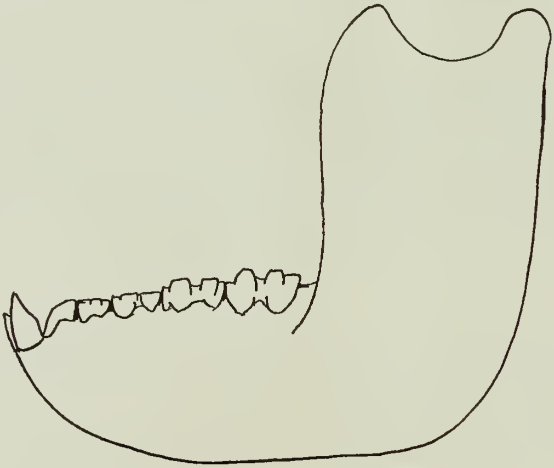


FIG. 16. Reconstruction of jaw from Olduvai IV, type of *Simopithecus jonathani* (Old. 1472, 57).

is rather more vertically disposed than that of the right side, which is angled more like that of the Kanjera baboon. The orientation of the rami in life was probably between that of the left and right sides as presently preserved; this shape is shown in Fig. 16, and does not differ significantly from the orientation of the rami seen in the Kanjera baboon, or for that matter, in *Theropithecus gelada*.

The symphysis shows a similar structure to that of the Kanjera and Olorgesailie specimens, and there is no mandibular fossa.

This specimen is said by Leakey and Whitworth to be female, presumably based upon the relative size of the canine, which is extremely worn, but which can be seen to have been somewhat larger, in cross-sectional area, than P_4. This is unusual for female baboons, in which the lower canine is usually the smaller in area. On the other hand, the tooth is small for a male, and the P_3 (also extremely worn), appears to have been short and scarcely sectorial in form. In view of the tendency towards reduction in the relative size of the male canine and P_3 which is characteristic of the genus, the possibility that the specimen is male cannot be altogether discounted, and is perhaps more likely than the usual attribution.

Teeth

Little remains of the crowns of the cheek-teeth in Old. 1472,57, although enough can be seen of P_4 and M_3 to make its generic identity reasonably certain. Although the incisors are absent, the bi-incisal breadth was clearly very small.

The teeth of M 14680 are well-preserved, and, with the exception of the dp_3, are unworn. The molars resemble those of the Kanjera form, but show all the peculiarities of the genus in exaggerated form. The foveae and clefts are all exceptionally broad and deep. The median buccal cleft is especially deep, and extends behind the protoconid and hypoconid, leaving these cusps standing as partially isolated columns. Similar grooves from the talonid basin and distal fovea cut behind the entoconid. As in one of the Kanjera M_3's the entoconid is divided into a double column, fully on M_2 and partially on M_1. The deep talonid basin is walled lingually by a horizontal enamel ridge which is clearly distinct from the lingual margin. M_1 bears an accessary capsule in the median buccal cleft.

The premolars are rather distinctive in structure, P_4 has a large and deep distal forea, but the mesial forea is extremely reduced. P_3 is of the usual form in male Cercopithecoidea, but is exceptionally short and broad, with a very short sectorial face contrasting with the extensive distal fovea.

The canine crown was not fully exposed, but clearly was small and low, especially as compared to the very large cheek-teeth.

The remaining Olduvai specimens cannot be assigned to a level in the sequence. They comprise:

a. M 19010

The inferior part of mandibular symphysis, broken slightly above the level of the 'simian' shelf. The muscular impressions representing the area of attachment of the platysma are rather strong; the inferior surface shows the usual *Simopithecus* shape.

b. 'Olduvai'

The superior end of a left ascending ramus, complete apart from some damage to the coronid process and the surface of the condyle. The sigmoid notch is shallow, and the condyle apparently shows typical *Simopithecus* features, such as the rather broad, flat, superiorly-facing articular surface, and a depression on the posterior surface of the condyle below the articular surface.

c. The posterior part of a left corpus, with part of the ramus. M_3 is present, its talonid somewhat damaged. Slight wear is present on the tips of all the cusps.

d. Old. 1952 GRCS 694

A fragment of a left horizontal ramus, with the second and third molars in place. M_2 shows moderate wear, M_3 is not fully erupted, and shows wear on the tip of the anterior lingual cusp only.

F. OMO

The series of formations along the lower Omo River, consisting of extensive and richly fossiliferous water-laid deposits, were described by Leakey (1943b) and Arambourg (1947), and have recently been more thoroughly surveyed by Butzer and Thurber (1969). Monkey material was collected and described by Arambourg, (1947) under the name of *Dinopithecus brumpti*. Re-examination of the specimens confirmed the view of Freedman (1957) and Leakey and Whitworth (1958) that they in fact represent a *Simopithecus* (i.e. *Theropithecus*).

Recent collecting in the Omo basin, (Howell 1969 and pers. comm.) has yielded a rich sample of material of Cercopithecoidea, some of which may be referable, or closely related to, *Theropithecus*. It seems not unlikely that these will be found to belong to the species represented by Arambourg's material. The latter comprises:

a. 'Type A'

The posterior part of a left maxilla, with M^2 and M^3. The second molar was fully in occlusion at the time of death, but is only light to moderately worn. The third molar was probably entirely within its crypt at death, but has been exposed by erosion of the alveolar surface. The root of the zygoma is present, and lies approximately above the midpoint of the second molar.

b. 'Type B'

A fragment of the right corpus of a juvenile mandible, containing the root of P_4, the first and second molars complete, and a fragment of the third. The first molar shows moderate wear, the second slight wear only, and the third was unerupted at the time of death, with the tips of the cusps just penetrating the bone of the alveolus. As in *Simopithecus* from other sites, the corpus is very robust at the level of the molars and their roots, but becomes rapidly thinner towards the inferior margin.

c. A fragment of a left corpus mandibulae, with a well-worn M_3.

d. Isolated dental specimens: the unerupted M_2, a worn M_1 and M_3.

The Omo teeth show no peculiarities to distinguish them from the type, Kanjera series, apart from the fact that one, at least, of the two M_3's evidently had a clearly defined tuberculum sextum. In size, they are very close to the female specimens from Olduvai I.

G. KAISO

The Kaiso deposits were described by Wayland (1926), Solomon (1939), and Bishop (1968). The major part of the formation consists of clays, silts and sands with few mammalian fossils. The fossiliferous layers from which the baboon specimen was recovered occur towards the top of the formation in the form of indurated sands, impregnated with ferruginous matter. According to Wayland, the clays were probably desposited during a pluvial period, while the sandy horizons formed during a period of dessication, and represent the site of shallow, drying pools. This view is accepted by Leakey (1951). Solomon and Bishop, however, argue that the clays were probably deposited under swamp rather than lacustrine conditions, and that the sandy horizons were deposited in more open water, with fluctuation reflecting tectonic rather than climatic factors.

The single monkey specimen from Kaiso is a maxillary fragment with right M^2 and M^3, both rather heavily worn. However, the structure of the crown, especially the existence of well-marked lingual and buccal mesial grooves, identifies the genus.

H. MAKAPAN

The geology of the Makapan ('Limeworks') site, situated close to Potgietersrus, Transvaal, has been described by several authors (Dart, 1925, 1952; Bosazza, Adie and Brenner, 1946; Barbour, 1949, King, 1951; etc.): the available evidence was summarized and greatly augmented by Brain (1958), and has recently been reviewed by Butzer (1970). The fossiliferous deposits, which have produced a rich mammalian fauna including *Australopithecus*, consist of the cemented filling of a subsidence-cavern, originally subterranean, in dolomitic limestone. Most of the fossils are derived from the 'Phase I breccia' (Brain 1958), believed to have been formed relatively gradually at a time when the cave entrance was small. It has been suggested (Dart, Brain, op. cit.) that the bones were accumulated at this period by carnivorous animals, (perhaps *Australopithecus*), and Dart (1957) has suggested that many specimens were used by *Australopithecus* in its osteodontokeratic culture. A sudden increase in the size of the cave-entrance was probably the cause of an abrupt change to the deposition of 'Phase II' deposits which include much surface material and few fossils; the latter are indistinguishable from those occurring in the Phase I breccia.

Skull

No original Makapan *Theropithecus* material was available for examination in the present study. It has, however, been fully described and figured by Freedman (1957, 1960), and casts of some of this material were examined.

The material as listed by Freedman consists entirely of cranial and dental fragments; no postcranial specimens are known. No upper jaw fragments are present. A number of teeth isolated or set in small jaw fragments complete the collection.

Fragmentary as it is, the material demonstrated that the Makapan form is clearly separable from the better known East African populations. As Freedman (1957,

1960) observed, the best preserved male mandible (M 626) shows a very distinct mandibular fossa, defined inferiorly by the strongly flaring lower border of the mandibular corpus. This feature is absent in the Kanjera and Olorgesailie forms. Traces of a similar fossa are to be seen in the female mandibular fragment (M 633), though it was evidently less well developed than in the male, as is usual in the females of species in which the fossa occurs. Furthermore, and also unlike the later East African series, the internal surface of the symphysis, instead of being flat, slopes downwards rather abruptly between the premolars again as noted by Freedman (1957, 1960). The shape of the mandibular corpus differs in another respect from that of the Kanjera and Olorgesailie forms. In the female specimen, in which the length of the molar row of 40 mm, the depth of the corpus below the median buccal cleft of M_2 is 38 mm (0.95 of molar length). In the Kanjera female M 11539 comparable dimensions are 42 and 29 mm, giving a ratio of 0·69.

The Olorgesailie and Olduvai I female jaws resemble that of Kanjera with ratios of 0·63 and 0·71, respectively. Among fossil forms, the closest approach to the proportion seen in the Makapan fragment is in the large female from Olduvai IV, with an index of 85%. A similar proportion (83%), was, however, seen in the only available female specimen of *T. gelada*. Although their relative depth at M_2 is similar, the shape of the corpus is rather different in the modern and the Olduvai IV form. In the Bed IV female, the inferior margin of the corpus is approximately parallel to the occlusal plane in the molar region, thus resembling the lighter-jawed Kanjera and Olorgesailie females. In *T. gelada* the inferior border diverges anteriorly from the occlusal plane, the corpus attaining its greatest depth below M_1. The Makapan female fragment is too incomplete for either of these shapes to be discerned, although it can be seen that its depth was greater below M_2 than M_1. In the male fragment M 626, however, the full depth of the corpus is preserved below M_3 and M_2, and the inferior border and the occlusal plane can be seen to diverge anteriorly quite strongly in this region. Thus, although the corpus is not fully preserved at the level of M_1, it can be presumed to have been considerably deeper than at the level of M_3. A similar shape is distinctive of males of *T. gelada*, but is not seen in Olorgesailie males, or the probable male fragment from Kanjera (M 11541), in which the inferior border of the mandible runs more or less parallel to the occlusal surface in the molar region, just as in females from these sites.

Teeth

These have been fully described and figured by Freedman (1957, 1960). Casts of some of Freedman's specimens were examined (M 2974, M 2967, M 2991, M 626, M 533). The molars, first described by Freedman, show the characteristics of the genus: accentuated fossae and clefts and marked asymmetrical hypsodonty. In a number of ways, however, they differ from those of the Kanjera form. In the upper molars the median lingual cleft is less well-developed, and V-shaped rather than rectangular in occlusal aspect, so that the lingual cusps are less well-defined columns. In the M^3 of M 2967 (Fig. 15 in Freedman, 1960), the mesial lingual cleft appears to have been, even in the unworn crown, relatively weakly developed. The whole buccal face of the tooth is very flat, with little of the columnar bulging of the buccal cusps typical of the genus. The medial buccal notch is a more open 'V', relatively shallow, especially as compared with the lingual notch.

Complementary differences are to be seen in the lower molars. As compared to Kanjera, the median lingual notch is less deep relative to cusp height, and is without 'beading' along its lingual margin. Because the talonid basin and distal fovea are less extensive, the entoconid is relatively larger, more conical and less columnar. The lingual margin, especially on the entoconid, is sharper. The median buccal cleft is not defined by a ridge, so that its floor is more continuous with the buccal face. In the M_3, the distal buccal notch is a more open 'V' than in the Kanjera form, and the distal fovea is smaller relative to the hypoconulid.

While these molar characteristics are not easily quantified, and each one is comparatively minor by itself, in sum they produce a tooth which is distinctly closer to the typical cercopithecine condition than is that of the Kanjera form, and which possibly may be considered more primitive.

The premolars do not appear to differ from those of the typical form, except that the sectorial face of the male P_3 is considerably more elongated relative to its breadth and to general dental size. This suggests that the upper canine of the Makapan form was more high-crowned than that of Kanjera, a prediction confirmed by the isolated, upper, male canine (M 2974), figured by Freedman (1960, Fig. 15) and attributed by him to *S. darti*. Although the specimen is worn, its height is still considerably greater than that of the virtually unworn Kanjera male specimen, and those from Olorgesailie. Its distal flange is also distinctly more prominent, producing a more bladelike form, which is honed to a sharp edge in its apical part. These characteristics of the canine-P_3 complex again approach *T. gelada* and the other large, living cercopithecines. On the other hand, the lower incisal region of M 626 is narrow, demonstrating as great a degree of incisal reduction as in the East African forms.

A final point of difference involves the wear on the molars. As noted, in Kanjera, Olduvai II, and Olorgesailie populations, individuals in which the third molar is erupting or in early occlusion invariably show severe wear on M_1 and a considerably worn M_2, producing a wear gradient from M_1 to M_3 which is more pronounced than in living Cercopithecinae. In the Makapan male (M 626) M_3 shows moderate wear, and had evidently been in occlusion for some time before death, but M_2 and M_1 show only moderate wear. In the Olduvai II female M 14953, by comparison, M_3 is erupting, M_2 is slightly less worn than the corresponding tooth in M 626, but M_1 is considerably *more* worn.

I. SWARTKRANS

Swartkrans, one of the cluster of early Pleistocene localities in the Sterkfontein valley, near Krugersdorp, Transvaal, has been described by Robinson (1952) and Brain (1958, 1970). The fossiliferous deposit, like the others in the district, consists of the cemented infilling of a cavern in dolomitic limestone, itself the result of subterranean solution.

The *Theropithecus* material from the site was extensively described and figured by Freedman (1957). All the described material is cranial and dental: a pelvis is mentioned by Freedman, but not described, and might equally well be attributed to *Dinopithecus ingens*.

About twenty specimens comprise the hypodigm, including a muzzle, some mandibular fragments and a crushed skull, all of females, and some male mandibular fragments.

From Freedman's description the Swartkrans form resembles the East African in most cranial characteristics; mandibular fossae are absent, the incisal region narrow and the temporal lines (in the female, and by implication in males also) meet well forward on the cranial vault. However, one at least of the Swartkrans females has a muzzle that is considerably higher anteriorly than those of the East African forms, and bears a deep maxillary fossa (Freedman, 1960). On the other hand, another Swartkrans female has no maxillary fossa, agreeing with the East African forms. As this feature is not generally so variable within populations of living Cercopithecoidea, the question arises of whether more than one form of *Simopithecus* occurs at Swartkrans. If this were so, they need not necessarily have been synchronic, since the filling of the cave is believed by some to have occupied a considerable space of time (Wolpoff, 1968).

The cheek teeth of the Swartkrans form do not differ significantly from the Kanjera sample in structure, and those specimens which were examined as casts do not show the supposedly primitive features seen in the Makapan teeth. The male P_3, however, is relatively longer than that of Kanjera, though not as extreme as in the Makapan male.

J. Hopefield

This open site situated off the arid western coast of Cape Province has been described by Singer (1962) and Singer and Keen (1955) and Keen and Singer (1956). The specimens, described in detail by Singer (1962), comprise a cranial vault, probably female, a number of cheek-teeth associated with a female P_3 and canine, a fragment of the posterior part of a massive mandible, several isolated teeth, and the proximal end of a radius.

The morphology of the cranial fragment agrees closely with that of Kanjera females, including such generically diagnostic features as the long and massive postglenoid process, and the narrow postorbital constriction. The corpus of the fragmentary mandible, though large and massive, is not deep.

The total range of dental size represented by the sample is considerable. While the smallest teeth and the cranium are comparable to females of the Kanjera form, the teeth of the large fragment can be matched only among males of the Olorgesailie and Olduvai IV samples. It is questionable whether such a range can be attributed solely to sexual dimorphism and intra-populational variability, and the possibility arises that more than one form may be represented, a possibility which can only be tested in the light of further material.

III. THE AGE OF THE *SIMOPITHECUS* SITES

The traditional framework for dating fossil sites in tropical Africa, the sequence of 'pluvial' and 'interpluvial' periods, believed to be correlated with the glacial and interglacial periods of higher latitudes, has been severely shaken by recent reappraisals (Flint, 1959). Although it is clear that climatic fluctuations have occurred widely in the African Pleistocene, it is quite uncertain how many such episodes should be recognized, whether they were synchronous throughout the region, and how far they can be related to glacial events.

Recent advances in geochronology are rapidly replacing the glacial-pluvial timescale with one based upon chronometric dates. While some of the *Simopithecus* sites can be situated directly on this scale, most must still be related to it on faunal, cultural and stratigraphical evidence.

The whole of the main Olduvai series was referred by Hopwood (1936, 1951, etc.) to the Middle Pleistocene. With better faunal evidence, however, it has become apparent that the deposits cover a very extensive period of the Pleistocene, a conclusion supported by the K-Ar dates of about 1·8 and 1·7 million years for the basal basalt and *Zinjanthropus* horizon of Bed I respectively. (Leakey, Curtis and Evernden, 1961; Hay, 1963). The length of the hiatus thought to occur within Bed II is unknown, although a Potassium-Argon determination from the lower part of the bed, below a prominent series of aeolian deposits, yields a date of 1·1 million years B.P. (Hay, 1963). Recent evidence from magnetic reversals suggests that the lower part of Bed IV may be as old as 700,000 years. In this case, the sites such as BKII in upper Bed II may be closer to one million years than to half a million as has been supposed (Grommé and Hay, 1971; M. D. Leakey, 1971). Bishop (1963) points out that a lengthy period of volcanic quiescence is indicated by the laterisation of hill-slope soils later incorporated into Bed III. How far this period is represented in the Olduvai sequence as a depositional gap is not known. On cultural grounds, the latest levels of Bed IV are unlikely to be older than 60,000 years, while the lower layers may be as old as 700,000 years.

The Kanjera deposits were dated by Leakey (1950) to the Kanjeran pluvial, which was named after them. This was correlated with the Riss glaciation of the European sequence, antedating 100,000 years B.P. (Oakley, 1966). Among East African sites he correlates Kanjera with the lower part of Bed IV, Olduvai. Oakley (1966) would, however, date Kanjera to about 60,000 years B.P., presumably largely on cultural grounds. The fauna, especially the elephantids (Maglio, pers. comm.) supports a general equivalence in age between Kanjera, Olorgesailie, and Olduvai Bed IV.

The Olorgesailie beds can be tied tentatively to the Olduvai sequence on cultural grounds. The human culture (Isaac, 1966b) is considered by Howell and Clark (1963) to be close to Chelles-Acheul 9, the third of five hand-axe culture stages occurring within Olduvai IV. Howell (1967) charts the Olorgesailie beds as spanning a time interval from 200,000 to 75,000 years B.P. The *Simopithecus* material is derived from a land surface approximately in the middle of the vertical sequence, and may thus be dated to about 120–100,000 years ago. The single radiometric date from the site (0·5 million years from an included, water-borne pumice) is unexpectedly high, and derivation from earlier deposits is suspected (Curtis, 1967). It is, however, consistent with the new evidence for the age of Bed IV, Olduvai, cited above.

Both Leakey (1943b) and Arambourg (1947) dated the Omo deposits to the earliest Pleistocene, antedating Olduvai. Leakey (1963) considered Olduvai I at least partly contemporary with the Omo beds, as did Cooke (1963). The recent Omo Research Expeditions (Howell, 1969, Butzer and Thurber, 1969); have broadly confirmed these conclusions, while greatly clarifying the stratigraphy of the Omo basin deposits and providing a series of radiometric dates. These show that the Omo beds of the earlier expeditions, now known as the Shunguru, Usno, Nkalabong and Mursi formations (Butzer and Thurber, 1969), do indeed immediately antedate Olduvai I, spanning a period from about 1·8 million years B.P. to an indeterminate base antedating 4·25 million years.

Early interpretations of the stratigraphical evidence which attributed the Kaiso fossiliferous beds to an interpluvial (Wayland, 1926), specifically the 'Kanjera-Kamasian' (Leakey, 1951), have been plausibly disputed (Flint, 1959, Bishop, 1968). Fuller investigations have shown the formation to be considerably thicker than anticipated, and perhaps to span several million years (Bishop, 1968). Faunal evidence, which has long led to the conclusion that formation as a whole was early in the 'Villafranchian' sequence (Leakey, 1951, Cooke, 1963) now suggests that it may have been deposited almost entirely within the Pliocene as currently defined, between about 5 and 2 million years B.P. (Bishop, 1968, Maglio, 1970).

The relative and absolute ages of the South African australopithecine cave breccias have been variously interpreted on petrological, faunal and stratigraphic evidence, and are still hotly debated. King (1951) attributed all the sites to a single depositional cycle, relying on geological evidence which Robinson (1952) and Brain (1958) showed to be misinterpreted. Brain's petrological studies led him to the conclusion (disputed, however, by Butzer (1970)) that breccias at neighbouring sites in the Sterkfontein valley were accumulated under different climatic conditions and therefore could not be contemporary, while the faunal evidence also suggests a long total span for the breccias (Robinson, 1952). Inferences about the sequence of formation of the breccias which were drawn on the grounds of correlation with the supposed pluvial-interpluvial sequence (Oakley, 1954a; Brain 1958), are no longer valid (Flint, 1959). While interpretations of the faunal evidence differ in detail (Oakley, 1954a; Howell, 1963), there appears to be general agreement with Cooke's (1963, 1968) position that they can be grouped into an early span which includes Makapan, and a later one including Swartkrans.

The dating of the breccias relative to sites elsewhere in Africa and to the chronometric scale presents peculiar problems (Tobias and Hughes, 1969), and at present relies almost entirely on faunal evidence. At one extreme the whole group has been assigned to the Middle Pleistocene (Kurtén, 1957), at the other, to the Upper or even Middle Pliocene (Broom, 1945; King, 1951; Robinson, 1952). Most authors appear to accept that the deposits are, as a group, of 'Villafranchian' age (e.g. Oakley, 1954a, 1966; Ewer, 1956; Brain, 1958; Howell, 1963; Cooke, 1963) however, recent chronometric determinations have shown that this supposed stage in Africa in fact includes faunas of a wide variety of Plio-Pleistocene ages. Cooke (1968) in a review of the faunal evidence suggests a broad equivalence between Swartkrans and Olduvai lower Bed II, which would suggest a date between two and one million years. Makapan is included in his 'Sterkfontein Faunal Span' which, however, includes sites now thought to range from about 1·5 million years (Olduvai I) to more than four million years (Kaiso). Furthermore, material from the still earlier sites of the Eastern Rift was not available for comparison at the time at which Cooke completed his revision. On present evidence it would seem that the breccias of the Sterkfontein Span might be distributed anywhere between five and two million years. A long and generally early timescale for the australopithecine breccias seems most plausible, and in the absence of chronometric dates is not contra-indicated by the high K-Ar date of Olduvai Bed I, as Leakey, 1963, seems to suggest.

Hopefield is rather securely dated, on faunal and cultural grounds, to the late Middle or early Upper Pleistocene (Singer et al, 1955; Cooke, 1963, 1968), later than Olorgesailie and Kanjera, and probably equivalent to, or rather later than, the latest layers of Bed IV Olduvai, with a chronometric date of about 50,000 years B.P. (Oakley, 1966).

The Koobi Fora site is reliably dated at close to 2·6 million years by K/Ar determination (Fitch and Miller, 1970). Ternifine is generally agreed to date from the

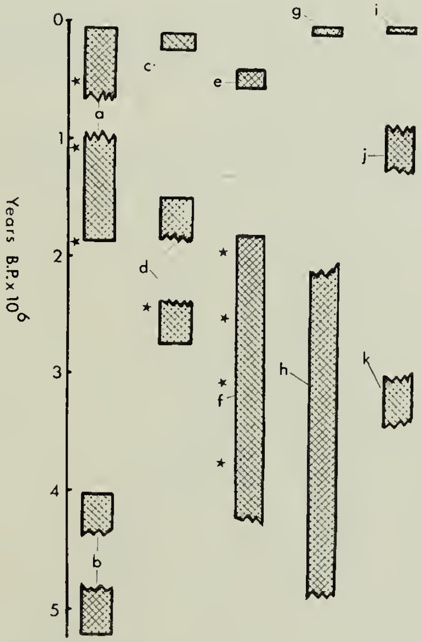


FIG. 17. Tentative chronological correlation of *Simopithecus* sites. a. Olduvai. b. Lothagam. c. Olorgesailie. d. East Rudolf. e. Ternifine. f. Omo. g. Kanjera. h. Kaiso. i. Hopefield. j. Swartkrans. k. Makapan. Stars indicate Potassium-Argon Age determinations. Note: Discoveries made since this diagram was prepared suggest that the Olduvai 'Upper' series is probably older than represented here, perhaps ranging from 1 to 0·4 million years B.P. (M. D. Leakey, 1971). By implication, Olorgesailie is also older than represented.

Middle Pleistocene, with a general equivalence in date to late Olduvai II, III or early IV. (Cooke, 1968). A suggested, tentative, correlation of sites with *Simopithecus* is shown in Fig. 17.

IV. THE SIZE OF *SIMOPITHECUS*

Simopithecus frequently appears in the literature as a 'giant baboon', while other authors have emphasized that the type (Kanjera) population consisted of animals no larger in body-size than some living baboons. Reliable evidence of body-size (derived from the post-cranial skeleton) is only available for the Kanjera and Olorgesailie populations. Using the results obtained on these series, it is possible to estimate the body-size of the remaining series on the basis of their jaw size.

Stature can be estimated within broad limits from the lengths of the long-bones. In the Kanjera form, these values are close to those seen in *Papio anubis neumanni* of similar sex. This is the living baboon of the Kenya Rift and Serengeti areas, and is slightly smaller than the typical *P. anubis* (Jolly, 1965).

The Olorgesailie form was obviously much larger than any living cercopithecoid. In the male, the humerus and femur (tibial and radial length are unknown) are comparable in length to those of chimpanzees or small female gorillas. In females they are shorter, roughly comparable to males of large forms of *Papio*, although the femur is relatively shorter than in that genus.

Body-weight was estimated on the basis of the hypothesis that it would be roughly proportional to the cross-sectional area of the humerus and femur, through which the weight is transmitted from the body to the ground in the quadrupedal stance. An expression of humeral and femoral cross-sectional area ('robusticity quotient') was derived by the formula (humerus shaft transverse breadth + anterior-posterior breadth)^2 + (femur shaft transverse breadth + anterior-posterior breadth)^2. Breadths were measured on the humerus at the level of the midpoint of the insertion of M. teres major, and on the femur approximately midway between the lesser trochanter and the distal end of the diaphysis. This value was calculated in several series of skeletons of extant Anthropoidea (*Papio, Mandrillus sphinx*). Ideally, values of the robusticity quotient should have been plotted against body-weight in a number of individual specimens weighed at the time of collection, but very few of these were available. A mean value of the expression was therefore calculated for each of the series, and plotted against a mean weight for the species derived from published sources (Snow, 1967, for *P. anubis*; Malbrant and Maclatchy, 1949, for *M. sphinx*). The regression so obtained is approximately linear (Fig. 18). The Kanjera and Olorgesailie limb-bone dimensions are projected on to the regression to yield an estimate of body-weight. Kanjera females are the smallest, with a body-weight in the neighbourhood of 20 kg, close to males of *T. gelada*. Kanjera males weighed about 35 kg, about the same as males of the largest extant forms of *Papio*. Olorgesailie males, however, probably weighed in the neighbourhood of 65 kg, as large as a female gorilla. In spite of this impressive size, however, they were far below the bulk of the male gorilla, which weighs at least 140 kg.

The body-size of the remaining series can be estimated only from the size of their jaws and teeth. An index of cheek-tooth area was therefore made for each of the *Theropithecus* samples by summating the products of the average length and breadth of P_4, M_1, M_2 and M_3. The regression of points derived from plotting these values against the weight of males as estimated from limb-bone cross-sectional area is approximately linear. Points derived from the series for which no limb-bones are available can then be projected on to the regression, to derive the estimates listed in Table 11. Needless to say, weights estimated in this way are subject to wide margins of errror, and can be regarded as approximations only. Nevertheless it is possible to state that the smallest Pleistocene *Theropithecus* was larger than the living gelada, and approached the largest living baboons in size, while the largest of them was a giant among Cercopithecoidea, as bulky as a small gorilla. Even the latter, however, was far less massive than male gorillas and, it may be surmised, than *Gigantopithecus*, which remain the largest primates known.

V. PHYLOGENY AND TAXONOMY

A. INTRAGENERIC DIVERSITY

The major parameters of variation observed between between fossil populations attributed to *Theropithecus* include absolute size, dental proportions and morphology, and facial and cranial shape. Unfortunately, not all of these can be documented in each sample.

Of the series described in the previous sections, Olorgesailie and Kanjera may probably each be considered as a sample drawn from a synchronous population.

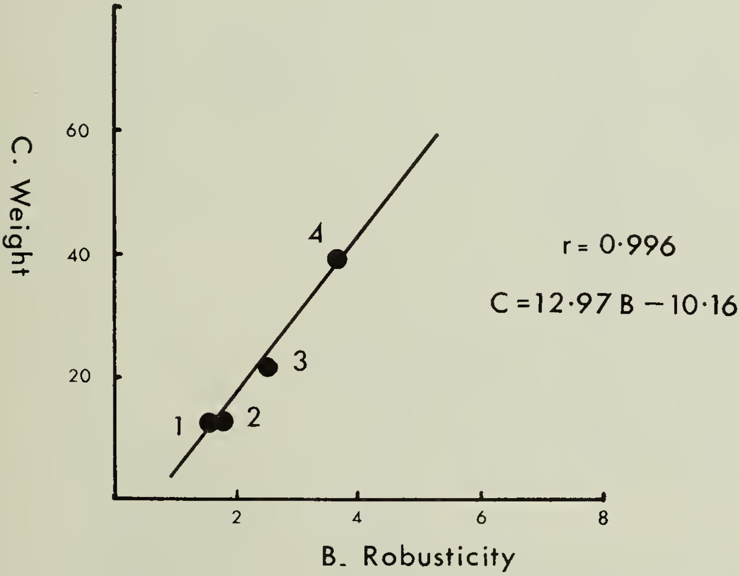


FIG. 18. Mean weight plotted against mean Robusticity Quotient in *P. anubis neumanni* males (point 3) and females (2), and *Mandrillus sphinx* males (4) and females (1).

TABLE II

Estimates of mean body-weight in *Theropithecus* populations, and data from which these were calculated

Form	A. Molar Area Quotient		B. Robusticity Quotient		C. Body-weight	
	Value (cm²)	Source	Value	Source	Value (Kg.)	Source
P. anubis neumanni, male	—	—	2·52	Mean of 2, USNM + AMNH	21·75±2·18	Snow, 1967 (N = 10)
,, ,, female	—	—	1·82	Mean of 3, AMNH + BMNH	12·32±1·24	,, ,,
Mandrillus sphinx, male	—	—	3·76	Mean of 3, AMNH	39	Malbrant, Maclatchy, 1949
,, ,, female	—	—	1·596	Mean of 3, AMNH	12	
T. gelada, male	4·10	Mean of 8, (AMNH + BMNH 24.8.7.5).	2·065	Mean of 2	16·62	Estimate from B
Kanjera male	7·10	Kanjera series	3·46	Kanjera series	34·72	Estimate from B
Kanjera female	5·90	,, ,,	2·39	,, ,,	20·84	,, ,,
Olorgesailie male	11·47	Olorg. series	5·63	Olorg. series	62·86	,, ,,
Makapan male	6·69	Makapan series	—	—	32·79	Estimate from A
Swartkrans male	9·36	Swartk. series	—	—	49·58	,, ,,
Olduvai IV male	11·88	M 14680	—	—	65·42	,, ,,

The Makapan and Swartkrans series were treated in a similar way, in the absence of evidence that the time-span during which they accumulated, while undoubtedly considerable, was significant against the scale of mammalian evolution. This view is not unchallenged (Wolpoff, 1970), and might be disputed on the grounds of the considerable range of variation in size and structure documented for both sites by Freedman (1957). Some of the Olduvai sub-series are related to a single site (such as BK II), and probably sample single synchronous populations. Others consist of specimens which are known to be broadly equivalent in age but cannot be treated as truly synchronic (e.g. the two specimens from Bed IV). The remaining series (Kaiso, Arambourg's Omo specimens, and the published Hopefield material) are too small and fragmentary to contribute significantly to establishing the evolutionary framework of the genus.

Previous authors have commented on the wide variation in absolute size within the genus. The size of the postcranial remains of Kanjera and Olorgesailie shows quite clearly that the latter was much the larger of the two. In the few cases where individual specimens of the series overlap this can be attributed to immaturity in the Olorgesailie specimen. Whereas the Kanjera animal was about the same size as the living chacma baboon (the largest form of living *Papio*), the Olorgesailie form was much larger than any living cercopithecoid (see section IV).

The same relationship is seen in cranial size. The juvenile frontal fragments from Olorgesailie are as large or larger than the equivalent parts in mature Kanjera males.

The few comparable cranial dimensions suggest that the Swartkrans form was somewhat larger than Kanjera, while Makapan was a little smaller.

These size-relationships are borne out by dimensions of the cheek-teeth (Table 4). In all but a few cases the smallest specimens of the pooled Olorgesailie series (which must be female) are larger than the biggest Kanjera males. Exceptions are the breadth of P^3 which is apparently as great in Kanjera as in Olorgesailie males, and the length and breadth of the female P_3, which is much the same in both samples.

Ranges of tooth-size in the Swartkrans, Kanjera and Makapan series overlap broadly, but suggest that Swartkrans was larger, and Makapan smaller, than Kanjera. Swartkrans dimensions overlap with those of Olorgesailie in such a way as to suggest that females of the East African form were about equivalent in size to males of the South African. Makapan overlaps with Olorgesailie only in P_4 breadth. The form from Bed I, Olduvai, is closely comparable to Swartkrans in dental size, but the upper Bed II form is larger, approaching Olorgesailie. Bed IV is larger still. The Omo material probably represents both sexes of a form about the same size as Swartkrans or Olduvai I. The Kaiso teeth might, by their size, have belonged to the Makapan form. As described earlier, the dimension of the Hopefield specimens suggest that two forms were represented in the sample, one about the size of Swartkrans, the other at least as large as Olorgesailie.

Statistical comparison of means of cheek-tooth dimensions is of limited value, since samples of teeth that could be realiably sexed were small, and reliable sexing is obviously a prerequisite of any statistical technique which involves the assumption that the sample is unimodally distributed. However, a few significant results were obtained using Student's t-test with Bessel's correction for small samples (Moroney, 1956). The mean of P^4 breadth is greater in Kanjera than in Makapan females, that of M_2 anterior and posterior breadth is greater in Swartkrans than in Kanjera females. In Makapan males the P_3 is significantly narrower than in Olorgesailie males, but both the South African forms had male P_3s that are significantly *longer* than those of the much larger Olorgesailie male. This expresses the difference between them in dental proportions.

Figs 10 and 11 show diagrammatically the means of tooth-dimensions in each sex and the four series. Both males and females show the order of increasing dental size Makapan-Kanjera-Swartkrans-Olorgesailie.

These observations suggest a general trend towards increasing size through the known history of the group, in so far as the earlier are the smallest, while 'giant' forms appear at the end of the sequence. However, the Kanjera series is both small and apparently late.

All the populations show the characteristic, complex and high-cusped cheek-teeth described above for Kanjera. However, there is interpopulational variation in the degree to which these characteristics are expressed. The large, late populations show greater crown complexity than the typical form, but this may in part be a size-related effect. The converse characteristics in the Makapan form, however, are probably truly primitive, and serve to link the genus with more typical Cercopithecinae. The most notable inter-populational variation in dental proportions is seen in the canines and anterior lower premolar of males. In the South African forms these teeth resemble their homologues in *Papio* males; the canines are high-cusped and blade-like, and the P_3 has a long, sectorial, mesio-buccal face. The canine-P_3 complex is especially large, relative to the rest of the cheek-teeth in Makapan males.

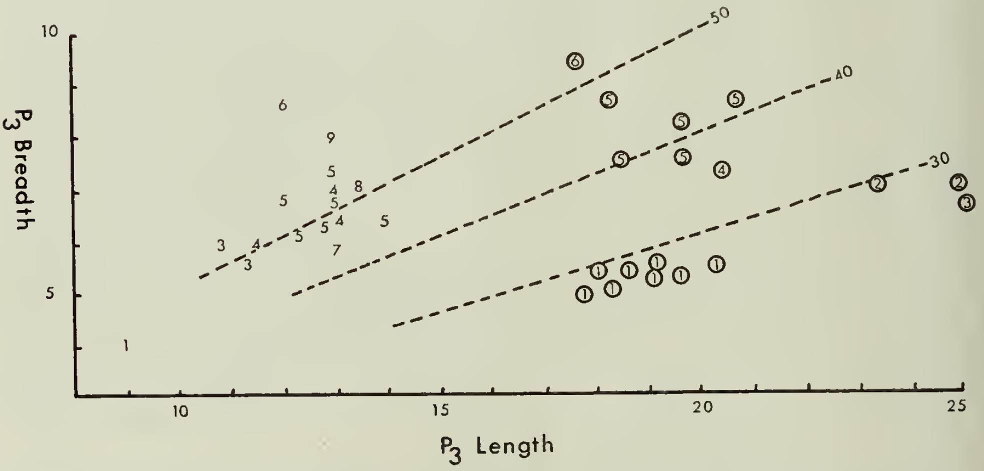


FIG. 19. Lower third premolar shape in *Theropithecus*. Breadth plotted against length with selected percentiles of Breadth/Length index. 1. *T. gelada*. 2. Swartkrans. 3. Makapan. 4. Kanjera. 5. Olorgesailie. 6. Olduvai IV. 7. Olduvai II. Males ringed, females unringed.

In Olorgesailie males the P_3 is strikingly short in comparison with its breadth (Fig. 20) and with the size of the cheek-teeth posterior to it (Fig. 10). Its shortness is due to a reduction in its mesio-buccal face, which in turn can be related to modifications in the upper canines, which are comparatively low-crowned and more circular in cross-section than those of a typical cercopithecoid. The Kanjera male, so far as can be judged from the rather small available sample, showed P_3 proportions and a canine size and shape intermediate between those of Olorgesailie and the South African forms (Fig. 19). The type of *S. leakeyi* Hopwood from Bed IV, Olduvai has an even shorter and broader P_3, and the tooth is as yet unknown in the other populations.

Fig. 20 shows the mean length of the male P_3 in the various fossil samples expressed by plotting it against the total length of the molars. There is a clear tendency for P_3 to become relatively shorter and broader in the later forms; its length is 50% of molar row length in Makapan, 45% in Swartkrans, between 30 and 35% in Olorgesailie, and less than 30% in the latest form, Olduvai IV. An apparent discrepancy is seen in the Kanjera form, which is closer to Swartkrans in proportions than to its supposed near contemporaries, Olorgesailie and Olduvai IV. The explanation might be that Kanjera is a primitive survival, or that the date of the site is earlier than generally believed. On the other hand, the fact that it was a much smaller animal than Olorgesailie and Olduvai IV suggests that its apparently primitive proportions might be due to allomorphosis. Such an effect is apparent in the P_3/molar relationship in extant *Papio*. As shown in Fig. 21, when mean length of P_3 is plotted against molar length, there are considerable inter-populational variations in proportions. Thus, male P_3 length in the very small baboon *Papio cynocephalus kindae* is about 45% of molar row length while in the large *P. ursinus* it exceeds 60%. However, as all points lie close to a straight line, the implication is that animals of all populations are affected by a single differential growth constant, the differences in proportion being due solely to variation in the length of the developmental span during which the growth constant is expressed in forms of different absolute size. (Freedman (1962b) found a similar relationship between calvaria length and facial length in *Papio*). The differential growth constant postulated for fossil *Theropithecus* is, of course, opposite in direction, with absolutely *smaller* forms having relatively longer P_3 and larger canine. As in *Papio*, however, the larger forms would show the apparently more specialized, and smaller ones the more primitive condition. A further implication of this hypothesis is that the differential growth constant itself was modified during the course of the evolution of the genus from a condition perhaps not unlike that seen in *Papio* to that seen in the advanced Pleistocene *Theropithecus*. This explanation of variability in the relative size of the canine-P_3 complex must be regarded as hypothetical pending the description of series of synchronic populations of different absolute size from time-levels other than the Middle Pleistocene.

The indications are that the shape of the skull, especially the facial part, showed considerably more inter-populational variation in fossil *Theropithecus* than did the structure of the teeth (cf. Ewer (1956) for a similar situation in fossil pigs). The Swartkrans form (or, perhaps, one of them if more than one is present) is distinguished from Kanjera, Olorgesailie, and Olduvai II by the relatively great height of the

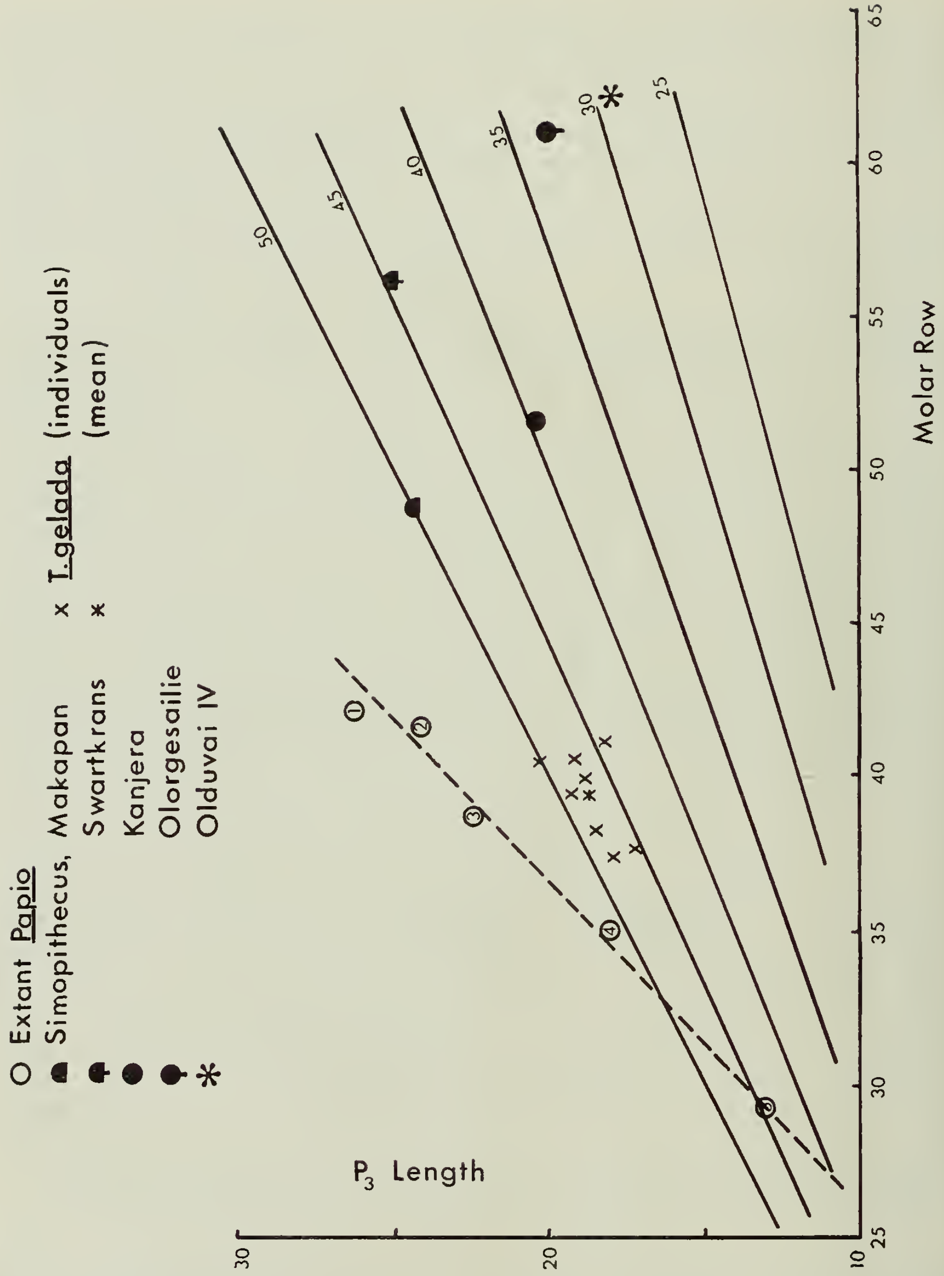


FIG. 20. Relative length of P_3 in males of *Theropithecus* and *Papio*. Mean P_3 length plotted against sum of mean lengths of three molars. Regression for *Papio* fitted by eye. (M_3 of Olduvai male is unknown; its length is estimated from the length of the female M_3).

anterior part of the muzzle (in females, at least) and by the occurrence of a maxillary fossa. Unfortunately the appropriate parts are absent from the other samples.

TABLE 12

Expressions of the relative height of the anterior muzzle in female *Theropithecus*

a = Height of muzzle anterior to third premolar
b = Length P^3 + Length P^4
c = Length M^1 + Length M^2

	a (mm)	b (mm)	c (mm)	$\frac{100b}{a}$	$\frac{100c}{a}$	$\frac{100b}{c}$
Swartkrans SK 563	46	16·0	28·6	34·8	62·2	55·9
Olduvai II M 18779	25·1	18·1	—	72·1	—	—
Kanjera M 14936	22	—	25·1	—	114·1	—
M 11537	20	14·1	25·1	70·5	125·5	56·2
T. gelada BM 24.8.7.5	14·2	10·6	20·4*	74·6	143·7	51·9

*Estimated, since M^1 absent

Mandibular fossae are known to be absent in Swartkrans, Olduvai II, Kanjera, Olorgesailie and Olduvai IV, and in some individuals of the Makapan sample. The male specimen (M 626) from Makapan, however, has an extremely deep fossa. The Olduvai I female has a slight fossa which probably indicates that the male of the form had a rather deeper one. The indications are therefore, that the possession of a fossa was a primitive character for the genus which was lost during the course of its evolution. In each of the later forms (Kanjera, Olorgesailie, Olduvai II, Olduvai IV) the internal profile of the symphysis is flat and scarcely excavated. Makapan again differs in showing a steeply-sloping symphysis, and Olduvai I is probably intermediate. The lateral profile of the mandibular corpus, more or less parallel-sided in the later forms, broadening from M_3 forwards in Makapan and to a lesser extent Olduvai I, shows, similar pattern of variation over time, and is perhaps related functionally and genetically to the last.

All the populations of fossil *Theropithecus*, apart from those represented by very small and incomplete samples, can thus be separated from one another on the grounds of size, or shape, or both. In translating this pattern of variation into the most likely phyletic tree connecting them over time we must bear in mind the likelihood of considerable polytypic variation, especially in size, within single species of widespread, terrestrial Cercopithecoidea, analogous to that seen in *Papio* (Jolly, 1965; Jolly and Groves, in preparation). Thus, unless populations differing in size and size-related characters can be shown to be strictly sympatric and synchronic we should hesitate to use their existence as evidence for the occurrence of cladogenesis. With few exceptions, the data are consistent with the view that all of the samples are representative of a single, polytypic but anagenetic phylum becoming progressively specialised over the course of its evolution.

There seems little reason to doubt that the Makapan *Theropithecus* was primitive, and could have been ancestral to later forms. The co-existence of different morphological types in the sample could be interpreted in several ways; it perhaps indicates a variable population which was in the process of losing the mandibular fossa, possibly it includes a mixture of specimens of different ages, representative of different populations along a chronocline, or, as a third possibility, it includes representatives of two synchronic species, rather similar in size, one of which retained primitive characteristics while the other was moving in the direction of later forms like Kanjera. While the third of the possibilities seems the most likely, one would not, without having examined the original material, insist on it in opposition to Freedman's view that all Makapan *Theropithecus* can be assigned to a single species.

The Olduvai I form, though imperfectly known, can be plausibly seen as a somewhat larger, more evolved descendant of Makapan, and Omo might well be similar. The Swartkrans sample again shows resemblances to Olduvai I in absolute size, and, although homologous parts are not available for comparison, seems to have departed to the same degree from the primitive condition seen in Makapan. It thus seems reasonable to assign all of them to different populations of a single lineage Further information is needed, however, especially about the height of the female muzzle, the occurrence of facial fossae, and the size of the male canine-P_3 complex in Olduvai I and the profile of the mandibular symphysis in Swartkrans.

There is little reason to question the derivation of the Olduvai II form from one resembling the Olduvai I and Swartkrans form. Equally there is nothing in its structure, as known at present, to disqualify it from a position ancestral to the Kanjera, Olorgesailie and Olduvai IV forms.

If Kanjera and Olorgesailie are truly contemporary, the question arises whether the considerable difference between them implies that they belonged to separate synchronic species. While a case could be made for specific separation, the view is here adopted that they more probably represent populations within a single, polytypic species. This interpretation is supported by the existence of considerable variation in size and size-correlated characteristics among populations of contemporary *Papio* which are not fully isolated genetically from one another.

Both in size and dental morphology, the juvenile fragment from Bed IV is appropriate to a more specialized population descended from Kanjera-Olorgesailie. The type of *Simopithecus jonathani* is clearly also a specialized representative of the genus, but its relationship to the previous specimen poses some problems. If it is indeed a female, as has been commonly supposed, then its general size suggests that it was drawn from the same population as the juvenile male, but its relatively large canine would indicate a completely new evolutionary trend not foreshadowed in any other population of the genus. If, on the other hand, it is a male, then its smaller size and extremely 'feminised' P_3 separate it from the juvenile male. There is apparently a possibility (R. E. Leakey, pers. comm.) that the *jonathani* jaw was derived from a gully-filling within Bed IV, and therefore dates from the extreme end of the main Olduvai sequence. If this is so, then it could be seen as representative of a very late, specialized population derived from that represented by the juvenile jaw.

The question of the coexistence of separate species of *Theropithecus* during the deposition of Olduvai IV will only be resolved with the description of new material precisely localized within the deposit.

It has long been recognized that the gelada baboon is the closest living relative of *Simopithecus* (Andrews, 1916). It shows, to some degree at least, all the distinctive features seen in the fossil forms: the large, high-crowned and complex cheek-teeth, the relatively small incisors, the relatively high and vertically orientated mandibular ramus, the forwardly-set temporal musculature, the high face with deep posterior maxilla, and the postcranial characteristics associated with extreme terrestrialism. While it is possible that the gelada has acquired these characteristics by parallelism, a view which is supported by the fact that they seem to comprise a single functional pattern (see below), the more economical hypothesis would seem to be that they are truly homologous. On the other hand, it seems unlikely that *T. gelada* is derived directly from *Simopithecus* of the Middle to Upper Pleistocene, from which it differs in having somewhat less specialized molar crowns (in particular, the trigon and talonid basins are less deeply excavated, so that the 'median longitudinal ridge' is a less prominent feature in the worn tooth), unreduced male canines and P_3, deep maxillary and mandibular fossae (the latter especially in males), a hollowed-out internal symphyseal profile, and a mandibular corpus which deepens towards the symphysis, again especially in males. In each of these characteristics the gelada resembles the condition believed to be primitive for the *Simopithecus* line, seen especially in the Makapan material, and progressively lost in later populations. Some of the apparent primitiveness of *T. gelada* may be due to its small size; for example, if our hypothesis about allomorphic influences upon relative canine size is correct, then a small form at any evolutionary stage would have had a relatively large male canine-P_3 complex. This is not, however, true of the facial fossae or the shape of the mandibular corpus and symphysis which seem more likely to be genuinely primitive. Two other features, however, ally *T. gelada* with late, rather than early *Simopithecus*. First, its anterior muzzle is even lower than that of the Kanjera form, and thus differs strongly from the early *Simopithecus*, if Swartkrans is representative of the latter. Second, its mandibular ramus is as vertically disposed and its temporal musculature as anteriorly placed, as in the later forms of Olorgesailie, Kanjera and Olduvai IV. Since the latter feature may be seen as functionally related to the dietary specialisation common to the whole genus (see below), it is not unlikely that it arose independently in *T. gelada* and the lowland forms. Other gelada characters, such as the narrow nasal aperture, the evenly concave facial profile, the pre-nasal tubercles, and the narrow, almost hemispherical premaxilla do not appear in either primitive or advanced forms of the *Simopithecus* line. The first may perhaps, as in local populations of *Homo sapiens* (Coon, 1965), be considered an adaptation to breathing the dry, cold air of high altitudes; the last may be associated with a unique gelada facial gesture – the 'lip-flip' displaying the pale, prominent mucous membrane of the premaxillary gum, and the lining of the upper lip.

The array of characteristics shown by *T. gelada* suggests that it is the result of an evolutionary line which diverged from that leading to the lowland fossil forms after the development of the basic adaptive pattern of the genus, but before the specialisation seen in the later forms had been acquired. This divergence might have occurred at any time subsequent to the differentiation of the genus, but probably was not later than Makapan times. It is not impossible that the population ancestral to

T. gelada was isolated in the Ethiopian highlands during the late Pliocene, and has never been more widespread. Certainly, all fossil material described from other regions subsequent to Makapan seems to pertain to the *Simopithecus* lineage.

Authors have differed as to the degree of taxonomic relationship appropriate to expressing the similarities and differences between the gelada and its lowland Pleistocene relations. Andrews (1916), describing *Simopithecus* on the basis of the Kanjera material, recognized its affinity to the gelada, but justified generic separation on the grounds of the length of the molars and the absence of maxillary fossae. Hopwood (1934), followed Andrews' definition. Dietrich (1942) regarded *Simopithecus* as a name uncritically applied to fossil baboons ancestral to *Papio*, and accordingly reduced it to a subgenus of the latter. His '*Papio* (*Simopithecus*)

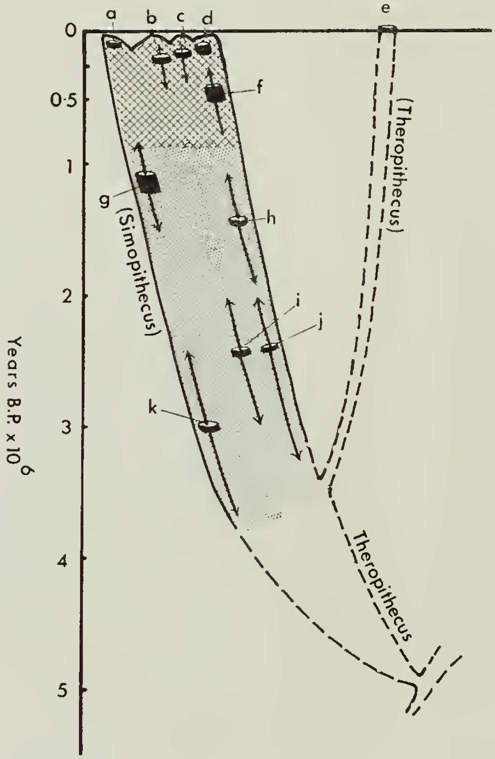


FIG. 21. Proposed evolutionary relationship of the subgenera and fossil populations of *Theropithecus*. The solid cylindrical segments represent the period of time over which each sample is believed to have accumulated. The arrows represent the probable range of possible chronological positions for each time-span. a. Hopefield. b. Olorgesailie. c. Kanjera. d. Olduvai IV. e. *T. gelada*. f. Olduvai Upper II. g. Swartkrans. h. Olduvai I. i. Kaiso. j. Omo. k. Makapan. Dotted: time-span of *T.* (*Simopithecus*) *darti*. Cross-hatched: time-span of *T.* (*Simopithecus*) *oswaldi*. Note: Information becoming available since this diagram was prepared indicates that the Olduvai, Upper II, Olduvai IV and Olorgesailie may be older than represented here. (See text.) (M. D. Leakey, 1971).

serengetensis' is however, a true *Papio* or *Parapapio*, not a *Simopithecus* or *Theropithecus*. Leakey and Whitworth (1958) list a number of dental and cranial characteristics from which they conclude that *Simopithecus* is distinct from other baboon genera, including *Theropithecus*. However, they base their diagnosis entirely upon the later, East African forms. DeVore and Washburn (1963) state flatly that '*Simopithecus* is probably *Theropithecus*', but do not justify their attribution. Most later authors (Jolly, 1966, 1967; Hill, 1970; Maier, 1970) have recognised the close relationship of *Theropithecus* and *Simopithecus* but have maintained full generic rank for each.

Almost all the diagnostic features quoted by Andrews (1916) and Leakey and Whitworth (1958) are either present also in *T. gelada*, or are absent, or variably present, in one or more *Simopithecus* populations. Apart from avoiding the difficulty of formally diagnosing *Theropithecus* and *Simopithecus* as separate genera there are major advantages to be gained from combining them in a single genus, which by priority must be called *Theropithecus*. First, it expresses the close cladistic relationship between the two lines while avoiding the necessity of groupings at the subtribal level, or of 'inflating' the whole taxonomy of the Cercopithecinae which genetically comprise a rather compact group. Second, and more importantly, it expresses, according to accepted palaeontological usage (Simpson, 1963), the fact that they share all the essential dental, gnathic and postcranial adaptive trends associated with a particular adaptive zone, unique to them among Cercopithecoidea. On the other hand, it is convenient to express in classification the hypothesis that *T. gelada* is descended from a separate branch of the genus, showing evolutionary trends rather distinct from those seen in the lineage including the known fossil forms. So long as this hypothesis holds, *T. gelada* may be classified alone in a nominate subgenus, while the known fossil forms may be assigned to subgenus (*Simopithecus*).

There is little agreement among authorities as to the number of species to be recognized in what is here defined as the subgenus *Simopithecus*. Several have been described: *S. oswaldi* Andrews 1916 from Kanjera; *S. leakeyi* Hopwood 1934 and *S. jonathani* Leakey and Whitworth 1958, both from Olduvai IV, and *S. danieli* Freedman 1957, from Swartkrans. *Papio darti*, Broom and Jensen 1946, and *Gorgopithecus wellsi*, Kitching 1953, both from Makapan, were recognized by Freedman (1957) as based upon material referable to a single species of *Simopithecus*. *Dinopithecus brumpti*, Arambourg 1947 (Omo) was also transferred to *Simopithecus* by Freedman (1957).

Freedman (1957), in the first major revision of the genus, regarded *S. oswaldi*, *S. darti* and *S. danieli* (which he proposed) as good species, defined morphologically, and later (1960) defended this view against Leakey and Whitworth (1958). The latter authors regarded the South African material, plus all that from East Africa, with the exception of the type of their new species *S. jonathani*, as representing a single species, *S. oswaldi*, within which they recognized separate subspecies, each occurring at a single site. Singer (1962) followed this scheme, suggesting that *S. jonathani* might also prove to be no more than subspecifically distinct.

The classification of the subgenus *Simopithecus* necessarily involves the arbitrary division of a continuously evolving lineage (Simpson, 1945, 1963), of which the earliest and latest representatives clearly merit specific separation. Since the Olduvai sequence is likely to provide the best time-related documentation of the evolution of the lineage at a single site, a convenient place to divide it is at a point corresponding to the depositional discontinuity in Bed II, believed to represent a general 'faunal break'. Populations preceding this break, at Olduvai and elsewhere, all show primitive characteristics and may be assigned to a single species for which the valid name is *Theropithecus* (*Simopithecus*) *darti* (Broom and Jensen, 1946), while those succeeding it can be regarded as chronologically and geographically dispersed subspecies of *T.* (*Simopithecus*) *oswaldi* In the absence of good evidence for co-existing species in Olduvai IV, *jonathani* is not accorded full specific status.

According to this scheme, the earlier species has a much larger time span than the younger. It is also much less well known; as more evidence accumulates it may well be expedient to break *T. darti* into more than one successional species.

Valid names are available for most recognizable subspecies of *T. darti* and *T. oswaldi*. If one form only is present at Makapan, it is the nominate race of *T. darti* (Broom and Jensen 1946). The type of this taxon is a male mandible lacking a fossa. If another, more primitive, form is also present, its valid *nomen* is probably *wellsi*, which was based upon the deeply-hollowed male jaw M 626. The Swartkrans form is clearly *T. darti danieli*. The early Olduvai form, considering its geographical distance, probably belonged to a separate subspecies, but cannot be diagnosed as such on present evidence, and may therefore be regarded as *T. darti* cf. *danieli*. The Omo form is also cf. *darti;* Arambourg's name *brumpti* is, however, available at the subspecific level if and when it is diagnosed, and might be applicable to the Olduvai I form also. The Kanjera subspecies is the nominate race of *oswaldi*. Leakey and Whitworth applied the subspecific name *mariae* as a *nomen nudum* to the Olorgesailie form; it is validated below (p 96) by diagnosis and the designation of a type.

The hypodigm of *leakeyi* Hopwood, 1934, was drawn from all three main 'populations' at Olduvai, (Beds I, Upper II, and IV) but its type is from Bed IV. Leakey and Whitworth used *olduvaiensis*, again without type or diagnosis, apparently as an objective synonym of *leakeyi*. There is therefore no valid name for the Olduvai II subspecies of *T. oswaldi*. No new name is proposed here, however, in view of the large amount of new material now becoming available which will enable a sounder diagnosis to be made at a later date. *Simopithecus jonathani*, Leakey and Whitworth, 1958 is provisionally treated as not separable from *T. oswaldi leakeyi*, on the conservative hypothesis that the type specimen is female. *S. oswaldi hopefieldensis* Singer 1962, based on the Hopefield material, is yet another invalid name which cannot be validated by a diagnosis on present evidence; the Hopefield form is here regarded as *T. oswaldi* subsp. cf. *leakeyi*.

Palaeotaxonomy faces a number of difficulties not encountered in the classification of living groups (Simpson, 1943). The most obvious of these is incompleteness of data; forms can be distinguished only on the basis of bones and teeth, while soft-part anatomy, pelage details and even repertoires of social behaviour, all of which are often of taxonomic relevance in Primates, must remain unknown. In the Anthropoidea in particular, the pelage tends to be variable and of taxonomic value at the specific and subspecific level (presumably because of the dominance of vision and hence of visual cues in species-recognition by the animals themselves). In the majority of cases, as with *Simopithecus*, not even the skeletal and dental record is complete, so that features of key importance are often unrepresented in a sample of material. In addition, fossil sites are disparate in space and time, so that phenomena like geographical clines, important in living species, are rarely demonstrable.

In view of these difficulties, the most that can be claimed for the classification of subgenus *Simopithecus* presented here is that it is consistent with the evidence at present available, and has certain advantages over previous schemes. Species are separated by morphological differences, especially by different patterns of growth and proportions of skull and dentition, while differences in size and size-correlated characters are considered to indicate no more than subspecific separation. Populations which are not widely separate in time, and which on the basis of the incomplete record might have been given either subspecific or full specific status have been given the lower rank. This arrangement is consistent with the natural history of *Theropithecus* as an open-country form which is unlikely to have speciated excessively as a result of geographical isolation, and corresponds to the situation in, for instance, extant *Papio*.

This scheme also seems more reasonable on *a priori* grounds than previous conceptions which united *Simopithecus* material from Olduvai I to IV, with a time-span exceeding a million years, into a single subspecies, yet separated Olduvai IV material from specimens from contemporary sites only a few hundred miles away. The present scheme agrees fairly closely with other faunal evidence connecting sites in East and South Africa, especially Swartkrans with lower Olduvai II, Hopefield with late Olduvai IV. It is also more consistent, of course, with the 'long' timescale at Olduvai.

B. Relationships of the Genus

It remains to investigate the relationships of *Theropithecus*, as here expanded, within the Cercopithecoidea. Le Gros Clark (1964) and Simpson (1963) have emphasized the importance of distinguishing adaptive trends rather than static 'characters' when assessing the relationships of organisms. In Cercopithecoidea it is important also to recognize the effect of allometric and ontogenetic trends. Neither of the latter has always been sufficiently appreciated in previous descriptions of *Theropithecus*.

The following developmental and evolutionary trends are characteristic of *Theropithecus* as a whole:

The crowns of the cheek-teeth become more complex: especially in larger forms. This evolutionary trend was well under way by the first appearance of the genus at Makapan and Lothagam 3, but continued throughout its development, at least in the *Simopithecus* lineage.

The molars and premolars become more high-crowned and relatively larger.

The incisors are absolutely small in all forms, and relatively smaller in the larger ones. This feature, and the contrast with *Papio*, is shown in Fig. 23, where the transverse breadth between the lateral faces of the alveolae of the lower, lateral incisors is plotted against the combined length of the first two lower molars.

The male canines are relatively smaller, and the 'sectorial' face of P_3 shorter, in the larger-sized forms at each evolutionary stage. This effect becomes intensified in the course of evolution. Allomorphic trends in the dentition are thus directly opposite to those seen in *Papio*, in which the largest forms have relatively as well as absolutely the largest canines, incisors and P_3.

The mandibular ramus becomes relatively higher. This trend can only be traced from Kanjera/Olorgesailie to Olduvai IV, if indeed this is a time-series. Both allomorphosis and evolutionary development are probably involved, but the material is not sufficient to assess the importance of each. In either case, the trend is opposite

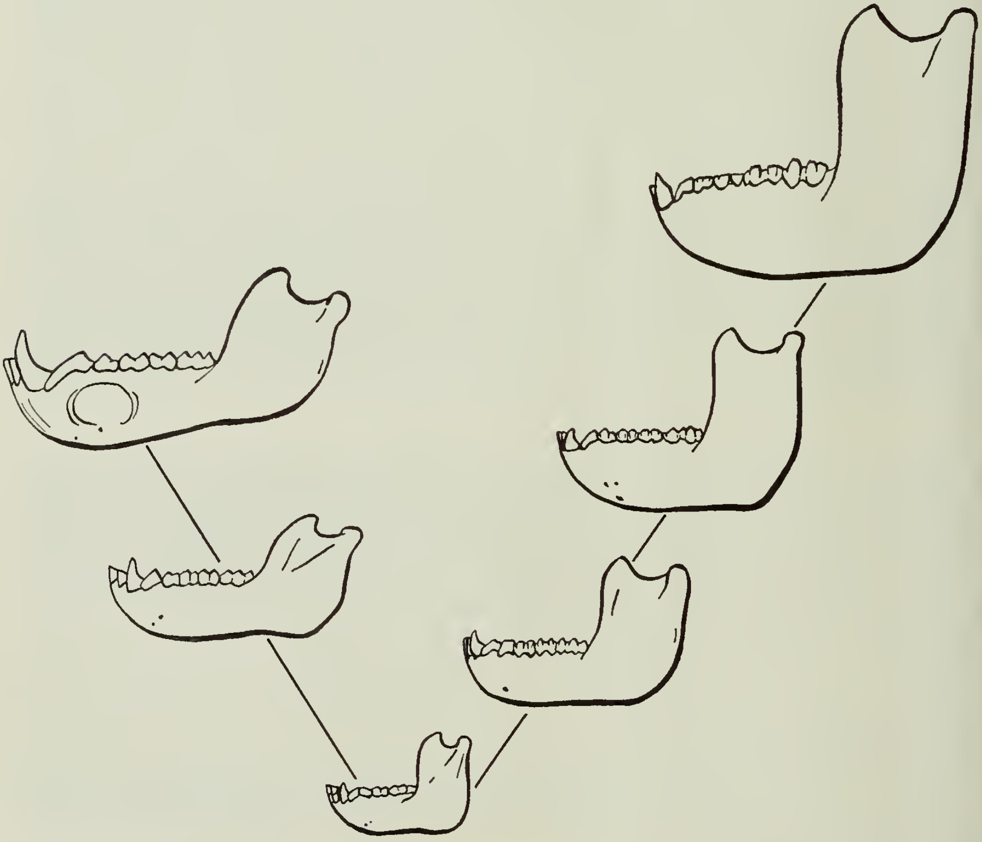


FIG. 22. Mandibular profiles of *Theropithecus* and *Papio*. Bottom: *Cercocebus torquatus* female (primitive shape in Papionini). Left line, ascending: *P. anubis*, female; *P. anubis*, male. Right line, ascending: *Theropithecus gelada*, female; *T. o. oswaldi*, female; *T. o. leakeyi*, female. Note contrasting allometric trends in two morphological series.

to that seen in other Cercopithecinae such as *Papio* in which the largest forms have the lowest rami, both absolutely and relative to corpus-length.

From the height of the ramus we can deduce that larger *Theropithecus* (especially at Olduvai IV) had a relatively larger glabella-prosthion dimension. This is also a feature of differential growth in *Papio* (Freedman, 1962b), and seems to be general in Cercopithecoidea (Jolly, 1965). In *Papio*, however, it is associated with an elongation of the basion-gnathion dimension, especially that part of it that is comprised of the tooth-row. In large *Theropithecus* the tooth-row is scarcely lengthened, but the posterior maxilla (and hence the mandibular ramus) is considerably deepened

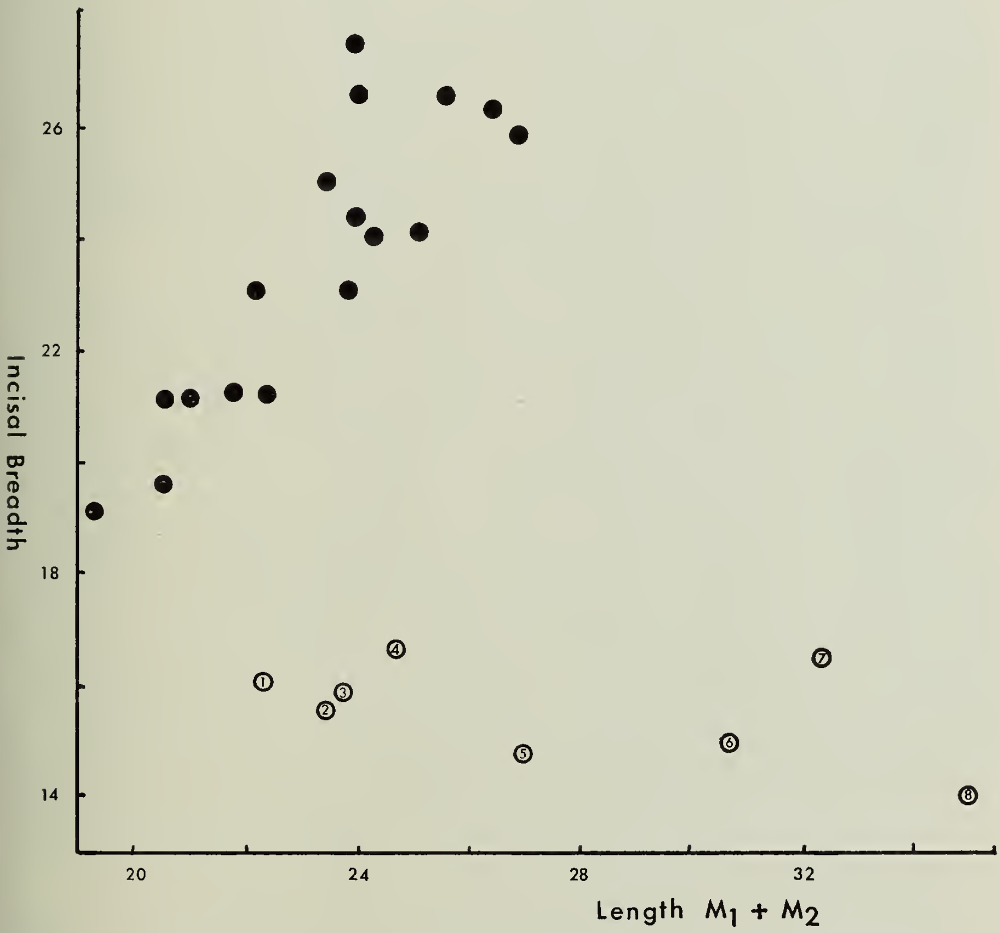


Fig. 23. Lower Incisal breadth plotted against combined length of M_1 and M_2. Open circles: *Theropithecus*. 1–3. *T. gelada* (males, AMNH). 4. Kanjera, ad. female (M. 11539). 5. Kanjera, juv. female (F 3398). 6. Olduvai IV, ad. female (*jonathani* type). 7. Olduvai II, juv. female (BK II). 8. Olorgesailie, ad. male (e). Solid circles: *Papio sp.* males and females, adults and juveniles, AMNH.

(Fig. 22). This difference in the shape of the maxilla may be partly due to the fact that the posterior molars are much larger, and apparently tended to erupt later, relative to the anterior dentition, in the large forms of *Theropithecus*. Thus, growth in the posterior maxilla might be expected to be prolonged, while that of the anterior part of the face was curtailed, when compared to forms such as *Papio*. Such a deepening would necessarily be accommodated by lengthening the vertical ascending ramus of the mandible. However, as described below, this feature may also be explained in functional and mechanical terms as a masticatory adaptation.

The temporal muscle originates relatively far forward on the braincase. Leakey and Whitworth (1958) quote the position of the meeting of the superior temporal lines ('at or about bregma in females, in front of bregma in males') as a character of *Simopithecus* distinguishing it from *Papio* in which they meet 'behind bregma'. This was questioned by Singer (1962), who rightly emphasised the variability of this character in *Papio*. There is, in fact, a valid distinction between *Theropithecus* on the one hand, and *Papio* and *Mandrillus* on the other, but it is less ambiguously defined in terms of ontogenetic process (Fig. 24). In all young Anthropoidea the temporal muscles are confined to the temporal fossa, from which they spread across the cranial vault as the jaws and dentition develop (Ashton and Zuckerman, 1956, Robinson, 1958). If growth continues after they meet in the midline, a sagittal ridge, then a crest, forms. Since the temporal muscles are known to grow even after sexual and dental maturity in *Papio* males, at least, (DeVore and Washburn, 1963), not even adults of like sex will necessarily show a similar pattern of lines and crests. *Theropithecus*, however, differs consistently from *Papio* and *Mandrillus* in the direction of temporal growth. The fibres spread fanwise from the temporal fossa, meeting first well forward on the cranial vault. The line of contact then lengthens back towards the inion and forwards to or beyond the bregma. This is the state reached in adult, Kanjera females. If further growth occurs (as in Kanjera males) a sagittal crest is formed along the line of contact. The crest itself is more or less even in height along its length, indicating uniform distribution of the temporal fibres. In *Papio*, growth in all but the earliest stages appears to be concentrated in the more posterior part of the temporal muscles. The temporal lines first meet at or very close to the inion. The line of junction moves only gradually towards the bregma as a sagittal crest forms adjacent to the inion. In *Mandrillus* the same growth-pattern is seen in a more exaggerated form. Here the posterior fibres of the Mm. temporales frequently meet at the inion early in their growth, but the sagittal crest, though it may become high and prominent, never advances more than two centimetres or so from the inion. The temporal lines in the region of the temporal fossa, and posteriorly well beyond the bregma, scarcely advance towards one another during growth, but frequently expand laterally to form, in adult males, broad flanges which roof the temporal fossae.

The forward position of the temporal muscles is certainly related to the vertical orientation of the mandibular ramus in *Theropithecus* and can also be related to the narrow postorbital region.

The short cranial base, with the transverse orientation of the auditory meatus seen in Kanjera *Simopithecus* may perhaps also belong to the same complex of features. If so, then the rather more oblique meatus of the Swartkrans and Olduvai II skulls might indicate that the trends towards vertical rami and forwardly located temporal muscles had advanced less far in these earlier forms. The evidence is tenuous, however, and needs to be supported by more complete skulls and mandibles from the sites concerned.

Although the height of its cheek-tooth crowns and orientation of the temporal musculature superficially recall the leaf-monkeys, there is no doubt that these

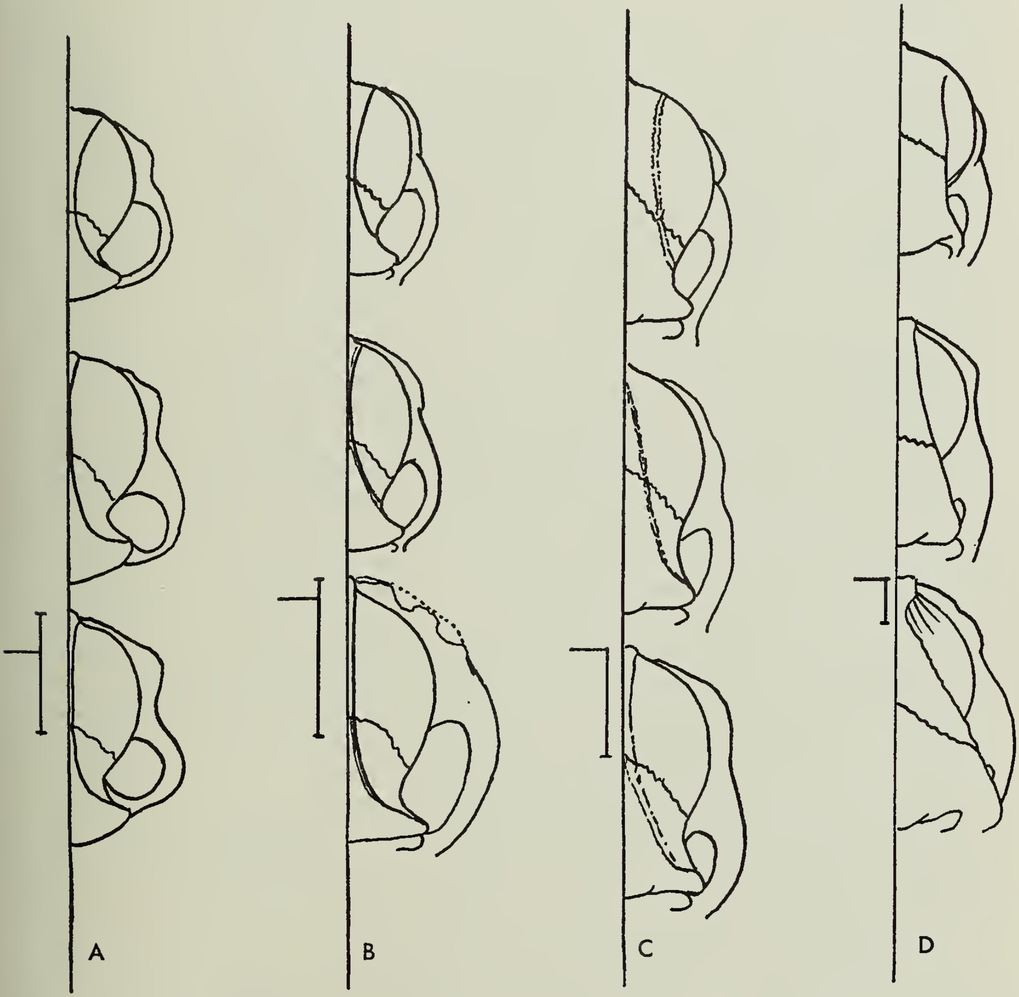


FIG. 24. Series of half-calvaria, from above, to show development of temporal lines and crests in large Papionini. A. *T. gelada*. Top to bottom: adult female, young adult male, old male. B. *T. o. oswaldi*. Sub-adult female, adult female, young adult male. C. *P. anubis*. Sub-adult male, adult male, adult male with exceptional crest. D. *Mandrillus leucophaeus*. Sub-adult male, adult male, old male.

resemblances are due to adaptive convergence, and that *Theropithecus* is, as has been universally recognized, allied with other Cercopithecoidea which have cheek-pouches but lack sacculated stomachs (Cercopithecinae of Simpson, 1945, Kuhn, 1967, Jolly, 1966, and most other authors; Cercopithecidae of Hill, 1966, following Pocock, 1925). Within this group, Garrod (1879), arguing from the structure of the liver, allied the genus with *Cercopithecus* rather than *Papio*, which would put it in the tribe Cercopithecini of Jolly (1966) and Kuhn (1967) (the subfamily Cercopithecinae of Hill, 1966). With this one dubious exception, the structure of *Theropithecus* from the molecular (Chiarelli, 1968, Sarich, 1971) to the behavioural (Crook, 1966) level, differs from that of the guenons and their allies, agreeing more closely with that of the remaining Cercopithecinae. Kuhn (1967) accordingly places the genus in his tribe Papionini (equivalent to Cynopithecinae of Hill, 1966) which includes all Cercopithecinae apart from the guenon group. Leakey (1965) presumably expresses a similar view by putting *Simopithecus* into the family Cercopithecidae, subfamily Cynocephalinae, which includes *Papio*, but is otherwise indeterminate. Jolly (1966) suggested that *Theropithecus* (and *Simopithecus*, which was regarded as generically distinct) should be put into a separate cercopithecine tribe, giving three co-ordinate groups: Cercopithecini, Cercocebini, and Theropithecini. It was recognized that the Theropithecini show many characteristics, such as a hypoconulid on M_3, chromosome number and details of the karyotype, indicating a common origin with the Cercocebini, but their many distinctive features were felt to merit more than generic separation. At the time, the natural history of the gelada was poorly reported and believed to be essentially similar to that of *Papio*; there was therefore no obvious functional explanation for its peculiarities, especially its extreme adaptation to terrestrial life, which could only be explained in terms of a long, separate evolutionary development. Recent studies by Crook (1966, 1967, 1968), however, have made it clear that most, if not all, the features that distinguish the gelada from other 42-chromosome monkeys are related functionally to its way of life, which is fundamentally different from anything seen in other living monkeys, not excluding *Papio* (see next section). If the peculiarities of *Theropithecus* are regarded as a single adaptive complex, they need not indicate a very remote separation of the lineage from other Cercopithecinae. It is therefore suggested that *Theropithecus* should be regarded as a rather distinct genus of the Cercocebini (=Papionini of Kuhn, 1967, which is the nomenclatorially correct *nomen*).

Hill (1968), in his rather more inflated classification of Cercopithecinae, retains Theropithecini as of Jolly (1966), but with the addition of *Libypithecus* Stromer, as a tribe *within* Cynopithecinae (= Papionini of Kuhn and this work) co-ordinate with tribes Cercocebini (macaques and mangabeys) and Papionini (*Papio*, *Mandrillus*, *Parapapio* and *Procynocephalus*). Without entering into discussion of the naturalness of the latter two tribes, which seems questionable, we might note that Hill's classification expresses a concept of the relative separateness of *Theropithecus* (*sensu lato*) from other 42-chromosome monkeys essentially similar to that suggested here.

At the other extreme, Buettner-Janusch (1966a, 1966b) has suggested that *Papio*, *Mandrillus*, *Theropithecus*, (and presumably *Cercocebus*) should be included in a single genus, *Papio*. This arrangement would imply the inclusion also of *Dinopithecus*, *Gorgopithecus*, *Parapapio* and *Procynocephalus* to produce a grouping coincident with tribe Papionini, as here accepted. Some of these fossil genera may well prove undefinable. Most are, however, better based than, for instance the many genera of mid-Tertiary Hominoidea which have recently been combined (Simons and Pilbeam, 1965). To lump them uncritically is to obscure the undoubted fact that the large, non-rainforest Cercopithecoidea, especially in Africa, showed much more diversity, and, by implication, much more ecological specialization, in the Plio-Pleistocene than is the case today. Part of the difficulty arises from the fact that the Cercopithecinae, like the Bovidae, are a group which has undergone extensive speciation and radiation comparatively recently. The problem lies in expressing this diversity in a useful and phyletically accurate way while not inflating the classification of the group to the point where it obscures the considerable similarity at the genetic level, which is manifested in their 'crossability' under artificial conditions, (Chiarelli, 1968). In the scheme adopted here a balance is struck by, on the the one hand, making genera of monophyletic groups of species sharing a common major adaptive trend (Simpson, 1963), while on the other, expressing the close genetic relationship between genera by grouping them in a single low level taxon, a tribe.

The interrelationships among the closely related genera within Papionini are not easy to deduce, much of the evidence being contradictory. Dental, cranial, genital and behavioural characteristics, for instance, suggest that *Papio*, *Mandrillus* and *Cercocebus* are more closely related to each other than to the rest, but chromosomal structure (Chiarelli, 1968) indicates that *Cercocebus* is distinct from the others. The describer of *T. gelada* (Rüppell, 1835) put it in the genus *Macacus* (i.e. *Macaca*). Certain behavioural traits (T. E. Rowell, pers. comm.) and the dispersed nature of the female 'sexual skin' (Matthews, 1956) recall macaques rather than living African Papionini. The unhollowed maxilla of late *Simopithecus* is also macaque-like, but is not primitive to the genus. Various authors, of whom Buettner-Janusch (1966) is the most recent, have allied *T. gelada* (and by implication fossil forms of the genus) with *Papio* (*sensu stricto*). Chromosomal structure (Chiarelli, 1968) is in accord with this view but anatomical evidence is not; their resemblances are superficial and easily accounted for by modest convergence, while those characteristics of *Papio* which are not related to its absolute size or terrestrial adaptation again ally it more closely with mangabeys and mandrills. Jolly (1966) suggested that *Dinopithecus* and *Gorgopithecus* might be placed in the Theropithecini because of resemblances to *Simopithecus* (= *Theropithecus*) in molar structure noted by Freedman (1957). Both are known only from South African sites, and have been described by Freedman (1957). Casts of some of the South African material were examined.

Dinopithecus is known from Swartkrans and Schurweberg, perhaps also Sterkfontein and Kromdraai. Its facial and cranial shape, length of muzzle and orientation of the mandibular ramus are such as might be expected in contemporary populations of the *Theropithecus* line, but its dental structure does not show the characteristic *Theropithecus* characters, and this separates it from *Theropithecus darti danieli* which is also found at Swartkrans (Freedman, 1957).

Gorgopithecus is found only at Kromdraai (Freedman, 1957), believed to be the latest and 'wettest' of the Transvaal australopithecine caves (Brain, 1958) Its molars are very like those of *Dinopithecus* but it has a shorter, deeply-hollowed maxilla, and, unlike most other Cercopithecoidea, including *Dinopithecus*, apparently lacks sexual dimorphism in general size, although the usual sex-differences in canines and P_3 are present. It shows no tendency to evolve in the direction of *Theropithecus*. *Dinopithecus* and *Gorgopithecus* thus seem to represent another line of Papionini, perhaps close in origin to *Theropithecus*, but evolving in a different direction. As far as is known, it left no descendants after the earliest Middle Pleistocene.

Perhaps the most reasonable view is that *Theropithecus* is an offshoot of an African papionine stock, which had already sent colonists (the ancestors of the macaques) to Eurasia, and which was later to give rise to *Papio*, *Mandrillus* and *Cercocebus*. The macaque-like characteristics of *Theropithecus* would thus be primitive, while those it shares with the African Papionini are due to a period of common ancestry.

The time of differentiation of the genus will undoubtedly be more clearly defined when more Cercopithecidae are described from the Pliocene of Kenya (Bishop and Chapman, 1970; Patterson, Behrensmeyer and Sill, 1970). At the present, the upper limit is set at about four million years by the occurence of a single *Theropithecus* molar at Lothagam 3 (Patterson, Behrensmeyer and Sill, 1970).

A taxonomic summary of *Theropithecus* follows:

Family: **CERCOPITHECIDAE** Gray 1821
Subfamily: **CERCOPITHECINAE**
Tribe: **PAPIONINI** Burnett 1828

Genus ***THEROPITHECUS*** Geoffroy 1843
GELADA Gray 1843; ***SIMOPITHECUS*** Andrews 1916;
BRACHYGNATHOPITHECUS Kitching 1952, in part

TYPE-SPECIES. *Theropithecus gelada* (Rüppell) 1835.

DIAGNOSIS: Differs from other Papionini by progressive development of the follwing characters: incisors small, and relatively *smaller* in larger forms; ascending ramus of mandible vertical, even in largest forms; ascending ramus of mandible *higher* in larger forms; molars and premolars large, broad, with high and complex crowns; postcranial skeleton highly adapted for terrestrial life; index finger very short. (Soft-part characters, known only in *T. gelada*, but probably part of the adaptive complex of the genus: sexual skin of females pectoral; accessory sitting-pads present; ischial callosities not confluent in males.)

DISTRIBUTION. Africa, mid-Pliocene to Recent.

Sub-genus: ***THEROPITHECUS*** (new rank)
Genus ***THEROPITHECUS*** auct.

TYPE-SPECIES. *T. gelada* (Rüppell) 1835.

DIAGNOSIS. A lineage of *Theropithecus* in which a somewhat primitive molar structure is retained, male canine and P_3 are scarcely reduced relative to the molars, deep mandibular and maxillary fossae are invariably present, especially in males, and the mandible deepens appreciably towards the symphysis. The superior surface of the symphysis is excavated. Specialisations of the sub-genus include: a high, convex premaxilla, narrow nasal aperture, and pre-nasal tubercles.

DISTRIBUTION: High plateau of central Ethiopia; Recent.

Theropithecus (Theropithecus) gelada (Rüppell 1835)

Macacus gelada Rüppell 1835; *Gelada rueppelli* Gray 1843; *Papio gelada* auct.

DIAGNOSIS AND DISTRIBUTION: As subgenus.

Subgenus ***SIMOPITHECUS***, new rank

Genus ***SIMOPITHECUS*** Andrews 1916, and most later authors

TYPE SPECIES. *Simopithecus oswaldi* Andrews 1916.

DIAGNOSIS: Lineage of *Theropithecus* distinguished from the typical subgenus by the following evolutionary trends: retention of primitive shape of premaxilla and nasal aperture; progressive loss of mandibular and maxillary fossae, reduction of male canine-P_3 complex; symphysis becoming shallower and less excavated superiorly, inferior border of corpus becoming more nearly parallel to occlusal plane; molars and premolars becoming even more complex. Body-build more robust. Tendency towards delayed eruption of third molars.

Theropithecus (Simopithecus) oswaldi (Andrews 1916)

Simopithecus oswaldi Andrews 1916; *Simopithecus leakeyi* Hopwood 1934 (in part); *Simopithecus jonathani* Leakey and Whitworth 1958.

HOLOTYPE. Female mandible, M 11537, from Kanjera; housed in the Department of Palaeontology, British Museum (Natural History), London.

DIAGNOSIS. More advanced than *T. darti*; maxillary and mandibular fossae are always absent or very weak, female muzzle lower anteriorly, male mandible not deepening anteriorly, superior surface of symphysis almost flat, male canine and P_3 relatively reduced, especially in larger forms.

DISTRIBUTION. Africa, from Cape of Good Hope to Algerian coast, Middle to Upper Pleistocene.

Subspecies: ***T. (Simopithecus) oswaldi oswaldi*** (Andrews 1916)

Simopithecus oswaldi Andrews 1916; *S. oswaldi oswaldi* Leakey and Whitworth 1958.

HOLOTYPE. As species.

HYPODIGM. Kanjera series, as listed above.

DIAGNOSIS. Small and somewhat less specialized than other known subspecies.

DISTRIBUTION. Kanjera.

T. (Simopithecus) oswaldi leakeyi (Hopwood 1934)

Simopithecus leakeyi Hopwood 1934 (in part); *S. oswaldi olduvaiensis* Leakey & Whitworth 1958; *S. jonathani* Leakey & Whitworth 1958; *S. oswaldi leakeyi* Leakey 1965

HOLOTYPE. Male mandibular fragment, M 14680, from Olduvai Bed IV, housed in the Department of Palaeontology, British Museum (Natural History), London.

HYPODIGM. Olduvai IV series as listed above.

DIAGNOSIS. Cheek-teeth much larger than in typical sub-species, somewhat larger than in *T. oswaldi mariae*. Male lower third premolar even more extremely reduced than in *T. oswaldi mariae*.

DISTRIBUTION. Olduvai IV, ? Hopefield (cf.)

T. (Simopithecus) oswaldi mariae subsp. nov.

Simopithecus oswaldi mariae Leakey & Whitworth 1958 (nom. nud.)

HOLOTYPE. An adult female mandibular corpus KNM–OG 0002, with complete cheek-tooth row, from Olorgesailie, labelled 'Site 10, Bed B, Tr. Fr.'; 'f' in descriptive list, p. 45. Housed in the Kenya National Museum, Nairobi.

HYPODIGM. Olorgesailie series, as listed above.

DIAGNOSIS. Body size and molar size larger than nominate subspecies, but smaller than *T. oswaldi leakeyi*. Male canine lower-crowned, P_3 shorter and broader than in *T. o. oswaldi*, but less extreme than in *leakeyi*.

DISTRIBUTION. Olorgesailie; ? Ternifine (cf.)

Theropithecus (Simopithecus) darti (Broom & Jensen 1946)

Simopithecus leakeyi Hopwood 1934 (in part); *Papio darti* Broom & Jensen 1946; *Brachygnathopithecus peppercorni* Kitching 1952; *Gorgopithecus wellsi* Kitching 1953; *Gorgopithecus darti* Kitching 1953; *Simopithecus darti* Freedman 1957; *Simopithecus danieli* Freedman 1957; *Simopithecus oswaldi* Leakey & Whitworth 1958 (in part)

HOLOTYPE. A damaged male mandible, M 201, 1326/1, housed at the University of the Witwatersrand, Johannesburg. (Freedman 1957).

DIAGNOSIS. A successional species ancestral to *T. oswaldi*, retaining primitive gnathic and dental characteristics, especially a longer male P_3 and high-crowned male canine. Female anterior muzzle probably also higher than in *T. oswaldi*.

DISTRIBUTION: ? late Pliocene to early Pleistocene, East and South Africa.

Subspecies: ***T. (Simopithecus) darti darti*** (Broom & Jensen 1946)

Papio darti Broom and Jensen 1946; *Simopithecus darti* Freedman 1957: *S. oswaldi darti* Singer 1962

HOLOTYPE. As species.

HYPODIGM. Makapan series ascribed to *Simopithecus darti* by Freedman (1957, 1960.)

DIAGNOSIS. Smaller than other subspecies, with characteristics recalling subgenus *Theropithecus*; primitive molar structure, high crowned male canines and long P_3, gelada-like symphysial profile and at least occasionally a deep mandibular fossa.

DISTRIBUTION. Makapan.

T. (Simopithecus) darti danieli (Freedman 1957)

Simopithecus danieli Freedman 1957; *S. oswaldi danieli* Singer 1962

HOLOTYPE. A female muzzle and two halves of the mandible from Swartkrans, SK 563/402/405, housed in the Transvaal Museum (Freedman 1957).

HYPODIGM. Swartkrans series ascribed to *S. danieli* by Freedman (1957).

DIAGNOSIS. Larger than nominate subspecies; dental and gnathic structure less primitive, tending towards *T. oswaldi*.

DISTRIBUTION. Swartkrans, Olduvai I and/or lower II (cf.)

VI. THE NATURAL HISTORY OF *SIMOPITHECUS*

The natural history of a fossil animal can never be completely reconstructed, but some conclusions about it can often be drawn from evidence of two main kinds. First, it is often possible, from a study of the context in which the animal is found as a fossil, to deduce in broad terms the climatico-vegetational zone in which it lived, and perhaps also to guess that particular surroundings within that zone were its preferred habitat. The context itself is divisible into two categories, the biotic and the geological. The first, the accompanying fossil flora and fauna, must be treated with caution since animals and plants from a variety of zones are not infrequently gathered in artificial association after death. The second, the geological context, is rarely unambiguous in its climatic implications (witness the 'pluvial' controversy).

The second major category of information is derived from the structure of the fossil animal itself, by recognition and interpretation of the adaptations of the form to its environment. It is important to distinguish between genetically-determined adaptations – fixed in the species by the action of natural selection – and the phenotypic adaptations made by the individual animal in the course of its lifetime of interaction with the environment. The distinction is important because inherited adaptations can persist in an ecological situation other than that in which they were evolved (the 'brachiator' characters of the mountain gorilla are a case in point), and hence give a false impression of the current way of life of the animal concerned. On the other hand, the existence of a genetically-determined adaptation in a species attest to a long period of selection under particular conditions, and hence are good evidence for or against long-term occupation of a particular ecological niche. In structures like bones which are relatively plastic to environmental influence even in the mature animal, it is often difficult to distinguish the effects of the two components of adaptation. In dentition the distinction should be easier; the major features of tooth size and cusp disposition may be assumed to be genetically-determined, while environmental effects are obvious in patterns of wear and perhaps such features as hypoplastic enamel bands. Interpretation of the anatomical evidence for the ecology of a fossil form rests very largely upon analogies drawn with living animals whose way of life is known.

The natural history of the Cercopithecinae varies widely among species. The range of the group as a whole includes all tropical vegetational types from rainforest to semi-desert *sahel*, and also various subtropical, warm-temperate and montane forests and woodlands. Within each broad habitat, different species show preferences for different kinds of country, and even forms that are sympatric are usually found on close study to exploit rather different aspects of their environment (Booth 1956, Hall, 1965). Some tropical rain-forest Cercopithecinae, and most of those inhabiting other vegetational zones, forage on the ground as well as in trees and are more or less adapted to terrestrial quadrupedalism. In a few species, most or all of the foraging time is spent on the ground; these have been distinguished as 'baboons' (Jolly, 1967).

Of particular relevance to reconstructing the natural history of Pleistocene *Theropithecus* is the ecology of the sole living representative of the genus, *T. gelada*, especially when this is compared with that of baboons of other genera, such as *Erythrocebus** and *Papio*. Early reports of the natural history of *Theropithecus* (Rüppell, 1835; Starck and Frick, 1958) have recently been supplemented by more detailed ecological data derived from prolonged field work (Crook, 1966, 1967, Crook and Aldrich-Blake, 1968).

The gelada is confined to the high plateau of Ethiopia, where it lives above the treeline. It is commonly associated with steep rock-faces and gorges, upon which it sleeps and takes refuge if attacked. Herds numbering up to 300 animals forage on the open, short-grass country, dissected by the gorges, where trees do not occur. Foods listed by Crook include a high proportion of rhizomes, blades and seeds of grasses together with stems and bulbs of other herbaceous plants. Fruits, bark, leaves and other tree products are rarely available and are scarcely exploited when they are. Like other Cercopithecinae, geladas eat small vertebrate and invertebrate animals when they come across them (P. Lisowski, pers. comm.) The gelada has a unique and characteristic way of feeding. Most of its time is spent in a sitting position, picking up small objects by hand using a precise, thumb-index grip, while shuffling slowly forward on its haunches. Frequently, areas of turf are torn up using both hands, to expose the roots. Crook plausibly suggests that the pectoral, rather than perineal, position of the female sexual skin is adaptive to this feeding position. The pair of fat-filled cushions situated ventral to the ischial callosities (Pocock, 1925) may be seen as further adaptation to habitual sitting on the ground while feeding.

Modern *Papio*-baboons are extremely widespread in trans-Saharan Africa, and inhabit all vegetational zones from semi-desert scrub to tropical rain-forest. Throughout their range they are opportunist and eclectic feeders. Forest-dwelling baboons of the Eastern Congo and parts of Uganda feed to a large extent upon the fruit of trees such as figs and *Maesopsis*. Those living under savannah conditions have been observed to climb *Acacia* trees to gather fruits and ant-galls. The feeding-methods of *Papio* are variable. When feeding upon small, concentrated objects such as grass-blades, it may sit, gelada-fashion, and pick them up, using both hands. A more characteristic feeding pattern, however, associated with larger but more scattered food-objects, is to stand 'tripedally', conveying food to the mouth with the free hand (Crook and Aldrich-Blake, 1968). On the ground, a wide variety of herbs is eaten, including blades and rhizomes of grass, tubers, seeds

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**Erythrocebus*, the patas monkey, is related phyletically to *Cercopithecus*, but is a baboon by the behavioural criterion (Jolly, 1967).

and fruits; parts of grasses make up the bulk of the diet of groups living in relatively treeless areas like parts of the Nairobi National Park (DeVore and Washburn, 1963). Animal food, consisting mainly of invertebrates and small vertebrates such as lizards, is regularly taken. Over the greater part of its range *Papio* is currently the only ground-living monkey, allowing it to exploit the full range of food-resources in its habitat. In much of the Sudanic belt and parts of East Africa, however, it shares its habitat with *Erythrocebus*, and the two forms exploit rather different aspects of the environment. The patas monkey is able to move independently of large trees and permanent water, and rarely enters the belt of trees that occurs along water-courses. *Papio* is typically to be found in the riverain strip in which it sleeps and from which it forages out into open country by day (Hall, 1965). More significant for the reconstruction of the Pleistocene ecology of the genus is its behaviour (described by Crook and Aldrich-Blake, 1968) in the small area of Ethiopia in which *Theropithecus* occurs. Here *Papio* is confined to woodland, and its diet includes a high proportion of tree-products. It does not occur in the open, treeless grassland inhabited by *Theropithecus*. Comparisons between *Theropithecus* (ancient and modern) and *Papio* in postcranial, cranial and dental anatomy are entirely consistent with the hypothesis that the same ecological distinction between the two genera existed during the Pleistocene, when both were equally widespread, and is the basis of the many adaptational trends which distinguish them.

A. HABITAT

The geological evidence of the climate of Olduvai in the Early and Middle Pleistocene is somewhat ambiguous. Hay (1963) emphasizes that minerals deposited among the lake sediments are indicators of dry climate with high evaporation rates throughout most of the history of the lake, producing saline and alkaline conditions in its waters. Leakey (1951, 1965) maintains that a *lower* evaporation/precipitation ratio than that existing in the region today would be necessary to account for the persistence of a lake throughout much of the Pleistocene, and points to the occurrence of frequent fish, crocodile and hippopotamus remains as evidence for the freshness of its waters. A likely explanation seems to be that while the main body of the lake waters may have been saline, fresh water occurred around the lake margins near the mouths of feeder-streams, and may have overlain the heavier saline waters over most of the lake surface. It would seem too that Lake Olduvai fluctuated widely in extent and salinity during its history, due to the complex interaction of variable evaporation, precipitation, catchment and drainage, the latter two factors being liable to alteration by tectonic movements.

Cooke's (1963) conclusion, that the Olduvai area was within the broad vegetational category between desert and rain-forest throughout its known history seems reasonable on faunal and climatic evidence. Variations in local climate probably produced vegetational fluctuations at most between semi-desert and moist, wooded savannah. The immediate faunal context has been reported for only one of the Olduvai *Theropithecus* sites – BK II, and is said by Leakey (1963) to imply 'lush vegetation'.

The Bed IV *Theropithecus* also lived, or at least was preserved as a fossil, in a waterside habitat, consisting of a flood-plain channelled by streams (Hay, 1963).

The geological and faunal context of *T. oswaldi* at Kanjera is essentially similar, with a lakeside setting and savannah fauna (Kent, 1942), and so is Kaiso.

The Plio-Pleistocene Omo beds were apparently laid down by the large, primaeval Omo River, and in the bed of the lake which it fed (Butzer and Thurber, 1969). Permanent, fresh water was undoubtedly present. The habitat is believed to have been not unlike that of the present day, with dense bush and gallery forest in the immediate vicinity of the river banks, giving way rather abruptly to drier and more open savannah-woodland (F. C. Howell, pers. comm.)

Isaac (1966b) describes the Olorgesailie basin at the time of its occupation by *Theropithecus* and Acheulian man. 'The fresh-water, mostly shallow, lake was normally surrounded by swamps and alluvial flats, which, from the evidence of root-channelling in the sediments appear to have been heavily vegetated with grasses and perhaps shrubs.' (p. 135) '. . . the seasonal stream-channels would have been the only bald patches in vast areas of thick grass and shrubs.' (p. 142). A higher rainfall, or at least a lower evaporation/precipitation ratio' must be postulated to account for the persistence of permanent fresh water in a basin which today supports only an intermittent swamp (Isaac, 1966a).

The climatic conditions existing at the time of the filling of the Transvaal caves have been reconstructed by Brain (1958), using petrological analysis. The Makapan fossiliferous breccia probably accumulated under conditions of 'some aridity', with a rainfall less than that of the present day, which is sufficient to support a 'bushveld' (Cooke, 1963). The Swartkrans breccia was apparently formed under conditions not far removed from those of the present, with 'temperate mixed grassland' the vegetational type (Cooke, 1963), though there is evidence for a minor dry oscillation within the deposit.

The sandy rock containing the Hopefield material is believed to represent the indurated remains of coastal dunes, among which lay vleis, shallow freshwater lagoons (Singer, 1962; Singer and Keen, 1955; Keen and Singer, 1956).

Pleistocene *Theropithecus* was clearly not confined to any one major climatic zone, ranging in latitude from the Equator to the Cape of Good Hope and the Algerian coast. Nor is it associated with any major vegetational zone, beyond the fact that none of its occurrences are among a tropical rain-forest fauna, an observation of dubious value since no such sites are known from this time period. It is striking, however, that wherever it is found, Pleistocene *Theropithecus* is associated with geological and faunal evidence for standing fresh water, usually shallow lakes surrounded by extensive alluvial flats and fed by sluggish rivers. By itself, this observation would be of little significance in reconstructing the ecological relationships of *Theropithecus* in the Pleistocene, since such depositional conditions are obviously ideal for fossilisation, as well as conducive to the accumulation of bones in ecologically meaningless death-assemblages. It assumes greater significance, however, if combined with the negative evidence of other sites at which *Theropithecus* is rare or absent. Table 13 is a list of the more important Plio-Pleistocene faunal sites in East and South Africa from which monkeys are reported. Group I are, from geological evidence, riverain, lake, or swamp deposits. All have hippopotamus, a good faunal indicator of fresh water. Group II sites are mostly caves, with no geological evidence for surface water nearby. Laetolil alone is subaerial. Hippopotamus is absent from Group II sites, apart from Makapan.

Table 13 also indicates the status of *Theropithecus* at each of the sites. It is either the only monkey, or the most frequent one, at all but one of the Group I sites. (The exception, Kanam, has yielded no baboon material at all, but only the remains of a single colobine monkey, as yet undescribed). It is completely absent from Laetolil and six of the eight cave sites. In the remaining two cave sites it is present, but outnumbered by other baboons, especially *Papio* and *Parapapio*. It may be significant that one of these two caves (Makapan) is the only one from which *Hippopotamus* has been reported, while of the three caves from which there are records of swamp-dwelling rodents, *Pelomys* or *Dasymys*, two are Makapan and Swartkrans.

Table 13

Indications of the habitat of fossil *Theropithecus*

	Thero-pithecus	*Papio/ Parapapio*	*Cerco-pithecoides*	*Gorgo-pithecus*	*Dino-pithecus*	*Hippo-potamus* sp.	*'Waterside' Rodents*
I 'Waterside' sites:							
Hopefield	A	—	—	—	—	X	
Olduvai I and basal II	A	—	—	—	—	X	
Olduvai Upper II	A	B	—	—	—	X	
Olduvai Upper IV	A	B	—	—	—	X	
Kaiso	A	—	—	—	—	X	
Kanam	—	—	—	—	—	X	
Omo	A	—	—	—	—	X	
Kanjera	A	—	—	—	—	X	
Olorgesailie	A	—	—	—	—	X	
Koobi Fora	A	—	—	—	—	X	
II 'Dry' sites:							
Taung	—	A	X	—	—	—	
Makapan	B	A	X	—	—	X	X[1]
Sterkfontein	—	A	X	—	X	—	
Bolt's Farm	—	A	X	—	—	—	X[2]
Gladysvale	—	A	—	—	—	—	
Swartkrans	B	A	X	—	X	—	X[2]
Kromdraai	—	A	—	X	X	—	
Laetolil	—	A	—	—	—	X	

Statuses:

(*Theropithecus*, *Papio* and *Parapapio*)*:*
A: Only, or most common monkey
B: Present, but less common than other form

Other monkeys, rodents and *Hippopotamus:*
X: Present

Data for monkeys from Freedman, 1957; other fauna from Cooke, 1963

[1] *Pelomys*

[2] *Dasymys*

From such evidence it seems reasonable to infer that *Theropithecus* populations living in the lowlands of tropical Africa during the Pleistocene frequented preferentially the alluvial flats surrounding shallow lakes and vleis. Such areas would, as indicated by Isaac (1966b) support a rich and dense ground-flora, especially grasses, but, being liable to season flooding, are unlikely to have been wooded or forested. There is thus a distinct parallel to the habitat-preference of *T. gelada*, which also avoids woodlands in favour of open grasslands.

B. ANATOMICAL INDICATIONS OF MOTOR HABITS

The available long-bones do not permit accurate limb-proportional indices to be calculated. Of the commonly used indices, the brachial index (Radius Length × 100/Humeral Length) and the humero-femoral index (Humerus Length × 100/Femoral Length) can be estimated for *T. oswaldi oswaldi*, and the latter for *T. oswaldi mariae*. There are however, no recognizable associated sets from single individuals, all bones have to be sexed by guesswork, and unbroken lengths estimated (section II). Errors arising are likely to be large and are compounded when the estimates are used to calculate indices. The values obtained for the indices must therefore be regarded as crude approximations only. Nevertheless, when these estimated dimensions are plotted against those of other Cercopithecinae, (Figs 25, 26), the data from both sexes of both subspecies are consistent in suggesting that *Simopithecus* was at the extreme edge of the range of large Cercopithecinae in its high humero-femoral, and low brachial index.

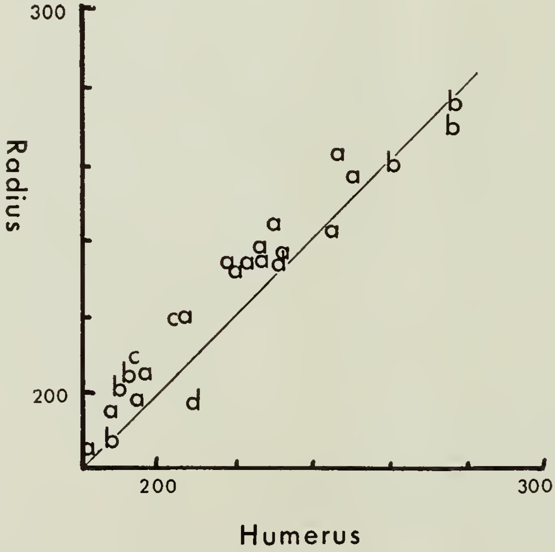

FIG. 25. Relationship between humeral and radial length in Papionini. a. *Papio*. b. *Mandrillus*. c. *T. gelada*. d. *T. owsaldi oswaldi*, male and female. Diagonal line represents humerus = radius in length.

TABLE 14

Limb-proportions in *Theropithecus*
The lengths of the segments in the fossil forms are estimated as described in the text

	Lengths (mm)			R/H	H/F	R/F
	Humerus	Radius	Femur			
Kanjera Large male	c 235	224	234	95·3	100·4	95·7
Kanjera Large female	209	198	201	94·7	104·0	98·5
Olorgesailie Male	c 290	—	297	—	c 97·6	—
Olorgesailie Female	c 240	—	232	—	c 103·4	—
T. gelada Male (U. Primatology)	194	210	209	108·2	92·8	100·5
T. gelada Male (AM 60568)	204	220	212	107·8	96·3	103·8

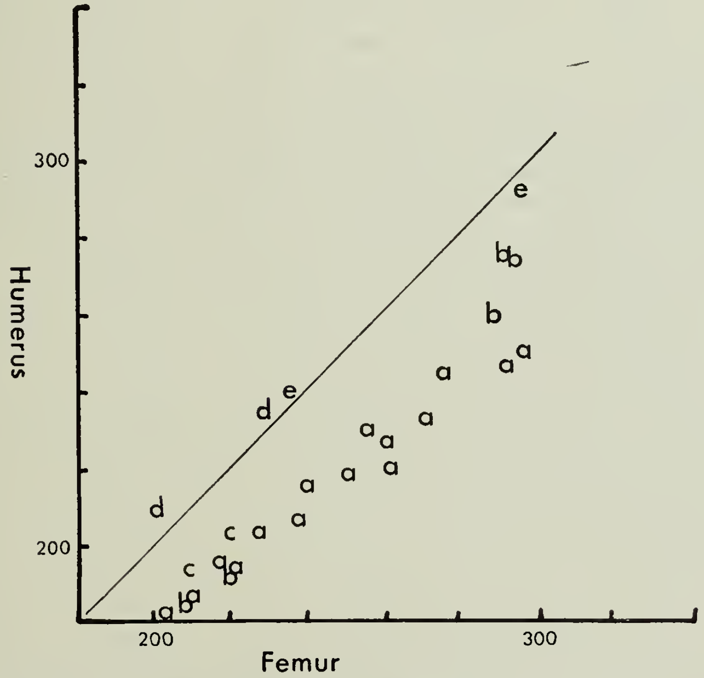

FIG. 26. Relationship between humeral and femoral length in Papionini. a. *Papio*. b. *Mandrillus*. c. *T. gelada*. d. *T. oswaldi oswaldi*, male and female. e. *T. oswaldi mariae*, male and female.

Among living Cercopithecinae, a tendency towards equality of femoral and humeral lengths is characteristic of terrestrial adaptation, especially among Papionini (Jolly, 1965). It is associated with an increase of the length of the upper arm, and of the arm as a whole, relative to the trunk length, as is presumably adaptive to locomotion predominantly upon level surfaces. The relatively long humerus of *Simopithecus* may be seen as a result of the trend carried to an extreme in a highly terrestrial form. However, it is also possible that its sedentary feeding habits were also a factor, especially since the robusticity of the femur indicates that the high index might be due to shortening of the thigh as much as to lengthening of the arm. In this connection, it may be significant that *Gorilla*, also a large, terrestrial, heavily-built, somewhat sedentary feeder, has the highest humero-femoral index among apes.

In its relatively short forearm. *Simopithecus* contrasts with *Theropithecus gelada*. In the extant Cercopithecinae, elongation of the fore-arm is associated with a terrestrial, cursorial gait, in both Papionini and Cercopithecini, presumably as an adaptation to fast running by lengthening the effective stride (Jolly, 1965, 1967). Among the Pongidae, the longest forearms are again associated with agility, but in this case it is acrobatic skills in climbing and brachiation that are involved, and the milieu is arboreal rather than terrestrial, the shortest forearm being found in the terrestrial but comparatively slow-moving gorilla. The short forearms of *Simopithecus* therefore do not conflict with the structural evidence for terrestrial habits, but simply reinforce the evidence of its robust skeleton that it was poorly adapted for rapid movement of any sort. In this it contrasts rather markedly with the living gelada.

It is possible to distinguish a number of features of the limb-bones of extant baboons which are correlated with adaptation to life on the ground. In most cases, it is also possible to suggest a plausible explanation of the characters in terms of advantage conferred in terrestrial locomotion (Jolly, 1964; 1967). Taken together, these characters form a single consistent functional pattern (Napier and Davis, 1959). Elements of this pattern are indicated by limb-bones of *Simopithecus* from each of the sites at which the post-cranial skeleton is represented.

The short, anteriorly curved femur of *Theropithecus oswaldi oswaldi* at once precludes the possibility that the animal could have been an active leaper, either arboreal or terrestrial. Among living monkeys it is closest to the gelada, but is tending towards the form seen in terrestrial Carnivora like the dog.

The humerus has a poorly-developed epicondylar flange, an indication that Mm. brachialis and brachioradialis were relatively weak as they are in the gelada and *Papio;* in *Mandrillus* and the large macaques the muscles and flange are much larger. The reduction of the elbow flexors in the baboons may be related to the fact that in ground-walking powered flexion of the joint occurs only during the recovery phase, when the flexors are acting merely against the weight of the forearm and hand, and so require no great power. In climbing, on the other hand, powered flexion also occurs during the propulsive phase, during which the whole body-weight is being lifted (Jolly, 1965), thus favouring large flexors in arboreal forms. The high Index of Articular Breadth seen in Kanjera *Theropithecus* and extant baboons is largely an expression of the relatively small size of the medial epicondyle in these forms, which perhaps, can be related to the relatively small size of the mass of flexor musculature, especially digital flexors, which originates from it (Table 15). Possibly the backwardly-folded medial epicondyle of the more terrestrial forms contributes to the stability of the elbow-joint when the forearm is in its habitual pronated position.

TABLE 15

Weights of muscles originating from epicondyles of humerus (in grammes, after dissection and saturation in 10% formalin solution)

	Theropithecus gelada	*Papio I*	*Papio II*	*Mandrillus sphinx*
Radial Epicondyle				
Ext. carpi radialis brevis	8·5	4·5	4·5	22·0
Ext. digitorum communis	6·5	4·0	4·0	18·0
Ext. digit. IV et V	2·0	1·5	1·5	5·5
Ext. carpi ulnaris	5·5	3·0	3·5	15·0
Supinator	3·0	3·0	3·0	11·5
Total, Radial Epicondyle	25·5	16·0	16·5	72·0
Ulnar Epicondyle				
Flex. carpi ulnaris	12·5	11·5	12·0	31·5
Palmaris longus	3·0	3·0	2·5	10·5
Fl. carpi radialis + Fl. dig. sublimis	18·0	15·5	15·0	81·5
Pronator teres	5·0	5·0	5·5	21·5
Total, Ulnar Epicondyle	38·5	35·0	35·0	145·0

The backward inclination of the olecranon process of the ulna is a very consistent 'baboon' feature that is also seen in non-primate terrestrial quadrupeds. It also occurs, unlike some other indications of terrestrial life, in *Mandrillus*. Functionally, it can be related to the action of the M. triceps brachii, whose three heads converge to insert by a common tendon on the tip of the olecranon. As the sole extensor of the elbow, the triceps group performs two functions during the propulsive phase of locomotion, whether climbing or on a level surface. While the limb is being powerfully retracted by its extrinsic musculature, and hence is acting as a propulsive lever (Gray, 1943), it must resist forces tending to flex the elbow. Then, during the final part of the propulsive phase, it gives a powerful axial thrust to the limb by extension of the elbow, the limb then acting as a propulsive strut, in Gray's terms. The crucial difference is that in level-surface locomotion the triceps is acting upon an elbow that is almost in full extension, while in climbing the elbow is rather strongly flexed throughout the movement, presumably in order to keep the centre of gravity of the animal close to the support. The triceps is obviously at its greatest mechanical advantage when its line of action is furthest from the axis of the elbow joint, that is, when it is perpendicular to the axis of the olecranon process. The greater the inclination of the olecranon, the higher the angle between arm and forearm corresponding to this position of maximum advantage (Fig. 27). Hence, the backwardly-inclined olecranon of the baboons is most advantageous in level-surface locomotion. The evidence thus suggests that the Kanjera *Theropithecus* was at least as terrestrial as extant *Papio*, and probably as ground-living as the gelada.

The Olorgesailie form shows the same characters of humerus, ulna and femur as the Kanjera. In addition, there is evidence of extreme terrestrial adaptation in the foot bones.

Among living Cercopithecinae it was found that the more ground-living the species, the shorter and stouter its proximal and middle phalanges of digits II–V, in both the hand and the foot. In Fig. 15 the robusticity of manual and pedal proximal phalanges is expressed by plotting their breadth against their length. In spite of the fact that phalanges of all digits except hallux and pollex are included, there is a clear progression in relative shortness almost without overlap, from the arboreal genera *Cercopithecus* and *Cercocebus* through *Macaca, Mandrillus* and *Papio* to the extremely terrestrial gelada. The phalanges of Pleistocene *Theropithecus* are even more stubby than those of its living relative. A second complex of features in the foot which is

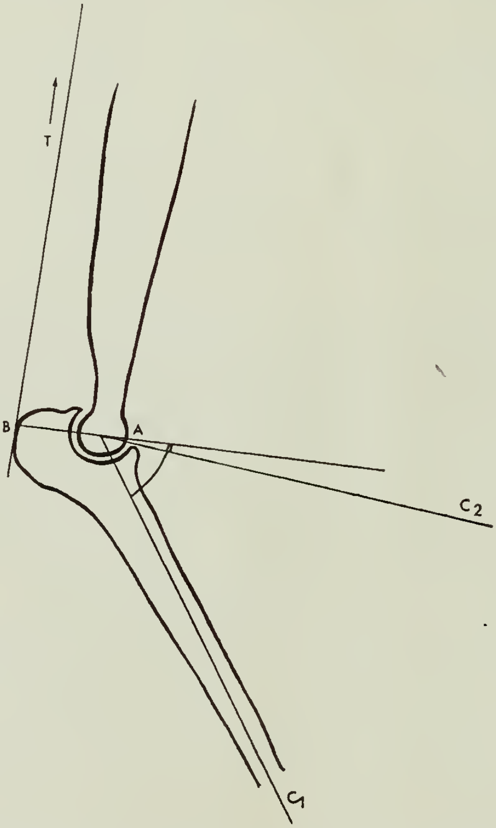

FIG. 27. Olecranon angulation and triceps action. Diagrammatic sagittal section through elbow. A. Centre of rotation of elbow joint. B. Midpoint of insertion of triceps tendon. T. Line of action of M. triceps. Triceps is at maximum mechanical advantage when angle ABT = 90°. AC_1 represents the corresponding position of the forearm in a terrestrial form with olecranon angle of about 60°; AC_2 the equivalent in an arboreal form with olecranon angle of about 10°.

related to arboreal or terrestrial adaptation concerns the relative size of the hallux and the muscles which power its movements, and its degree of abductability, all of which are greater in tree-climbing than terrestrial monkeys (Pocock, 1925, Midlo 1934, Gabis 1960; Jolly 1965). Unlike the proportions of the phalanges, the relative development of the hallux is evidently dependent upon the absolute size of the animal, as well as upon its degree of arboreal adaptation. Thus, the largest and most powerful halluces in the Cercopithecinae are to be found in the larger monkeys such as *Mandrillus* and *Macaca nemestrina* which are in other ways only moderately adapted to tree-climbing. Among animals of approximately equal body-size, the size and power of the hallux is proportional to degree of arboreal adaptation; thus, *Mandrillus* has a larger and more powerful hallux than *Papio*, and *Papio* than *Theropithecus*, and a similar relationship is seen between *Cercopithecus* and *Erythrocebus*.

Reduction in hallucial size, abductability and power in the baboons, especially in *Theropithecus*, is expressed in a variety of characters of the hallux itself, the structures in the tarsus which support it, and the relative size of the muscles which move it. The hallucial metatarsal itself is small and weak, as compared with the axial metatarsals III and IV about which the terrestrial foot is organized. The distal articular surface of the first cuneiform, which supports it, is relatively small and thus scarcely extends as a 'beak' dorsal to the body of the bone (Fig. 28). In turn, the articular facet on the second cuneiform that articulates with the 'beak' is itself small (Fig. 12) as is the superior of the two facets on the medial face of the base of the second metatarsal, which has a similar function. In the gelada (though not *Papio*) the distal articular facet of the first cuneiform scarcely extends on to the medial surface of the bone, indicating some loss of abductability of the first metatarsal (Fig. 28).

Each of these skeletal characters is observable in the *Theropithecus* material from Olorgesailie, and the shape of the distal facet of cuneiform I is as restricted as it is in the gelada.

The weakness of the baboon hallux, especially that of the gelada, was reflected in the size of the muscles powering its movement in the small series of specimens

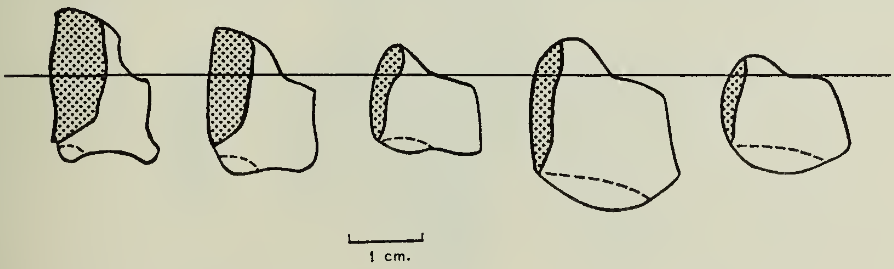

Fig. 28. Right medial cuneiform, medial aspect. Left to right: *Mandrillus leucophaeus*, male; *Papio anubis*, male; *Theropithecus gelada*, male; *T. oswaldi mariae* (2). Note: a. Relative size of distal articular surface, and its extension on to the medial aspect. b. Relative size of dorsal 'beak' (above horizontal line). Area of attachment of M. tibialis anterior tendon within dotted line.

dissected. Both the major Mm. peronei (M. peroneus longus and M. peroneus brevis) are, in the Cercopithecinae, plantarflexors and evertors of the foot. M. peroneus longus, inserting into the lateral side of the base of the first metatarsal, is in addition a powerful adductor of the hallux at the metatarsal-cuneiform joint. In the gelada M. peroneus longus was slightly less in weight than M. p. brevis. In *Papio*, longus was twice as massive as brevis, while in *Mandrillus* it was three times as heavy, reflecting closely the relative size of the hallux in the three forms. A similar relationship is seen in the antagonists of the peronei, the two parts of M. tibialis anterior. In the monkeys dissected, as well as in the rhesus monkey (Howell and Straus, 1933) the two parts were almost completely separable. Both originated from the lateral surface of the tibia and the adjoining part of the interosseous membrane. Each gave rise to a tendon passing beneath the transverse crural ligament. The tendon of the larger part of the muscle inserted upon the plantar and medial surfaces of the first cuneiform, into a prominent tubercle immediately posterior and inferior to the distal articular surface. The tendon of the lesser portion followed a similar course, but inserted into the medial side of the base of the first metatarsal. Both parts are so placed as to be dorsiflexors and invertors of the foot. The lesser portion (sometimes termed M. abductor hallucis longus) is also in a position to produce abduction of the first metatarsal, as the particular antagonist of the M. peroneus longus. As might be expected, the M. abductor hallucis constituted a greater fraction of the total tibialis anterior mass in those forms with the largest hallux, while its relationship to its antagonist was rather constant throughout the series (Table 16).

The proportions of the major peronei and the parts of tibialis anterior cannot, of course, be directly observed in *Simopithecus*, but several details of the tarsus and metatarsus indicate that these were much as in the gelada, or even more extreme. A small peroneus longus is indicated by the absence of a large tubercle of attachment on the base of metatarsal I, and even more clearly by the relatively small facet for the peroneus longus sesamoid on the cuboid. On the other hand, a large peroneus brevis is indicated by the massive peroneal tubercle on the base of metatarsal V. There is no direct evidence for a small abductor hallucis longus, but the peculiar convexity of the inferior border of the first cuneiform (which was not seen in any of

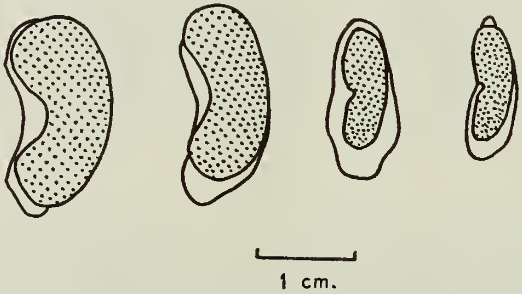

Fig. 29. Right medial cuneiform, distal aspect. Left to right: *M. leucophaeus*, male; *P. anubis*, male; *T. oswaldi mariae*; *T. gelada*, male.

TABLE 16

Weights of two parts of M. tibialis anterior and of the two major peronei (in grammes, after dissection and uniform saturation in 10% formalin)

	T. gelada	*Papio I*	*Mandrillus sphinx*
Tibialis anterior			
Major part	8·5	14·0	19·5
Abductor hallucis longus	1·5	3·0	7·5
Total	10·0	17·0	27·0
Peronei			
P. longus	4·5	8·0	20·0
P. brevis	5·0	4·0	6·5
Total	9·5	12·0	26·5
P. longus as % of total peronei	47·4	66·6	75·5
Abd.hall.long. as % of Tib. ant.	15·0	17·6	27·8
Abd.hall.long. as % of peron.long.	33·3	37·5	37·5

the 'living' series) could be interpreted as a greatly enlarged tubercle of insertion of tibialis anterior (proper).

The selectional advantage of a long and powerful hallux, and long pedal digits, to animals which habitually run along and climb branches is not difficult to find. In branch-running the transverse base of the animal is always narrow, so that the weight-line is easily displaced outside it. When this happens, a powerful turning

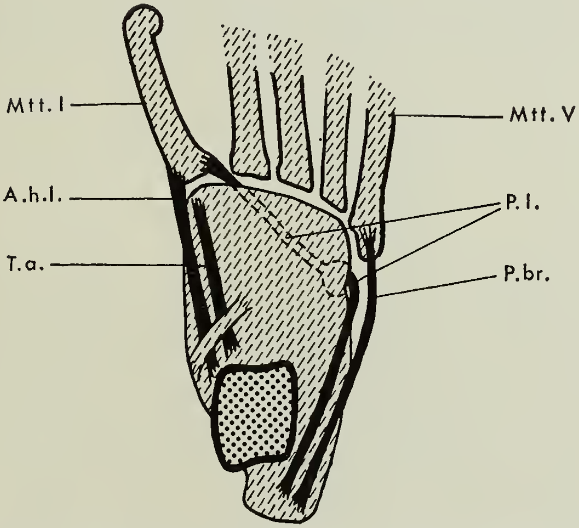

FIG. 30. Diagram of dorsal aspect of right tarsus, showing arrangement of tendons of Mm. tibialis anterior (T.a.), abductor hallucis longus (A.h.l.), peroneus longus (P.l.), and peroneus brevis (P.b.), and their insertions. Mtt. I = Hallucal metatarsal; Mtt. V = Fifth metatarsal.

couple is exerted tending to topple the animal from the branch (Fig. 31). The moment of the couple is Wh, where W is the weight of the animal and h the distance by which the weight-line is displaced. If the animal is not to fall, this couple must be resisted by an equal and opposite frictional couple exerted by the extremities, especially the feet. This frictional couple, in turn, is determined largely by the diameter of the branch spanned (d), and the amount of pressure that can be exerted normal to the branch surface by the action of the digital flexors and hallucal adductors (V_1 and V_2). Long phalanges in digits II–V, and a long and abductable hallux increase the possible size of d, while powerful flexors of the digits and adductors of the hallux increase V_1 and V_2, respectively. The apparently disproportionately large hallux of the mandrill and other big, semi-arboreal monkeys, can be accounted for by the fact that while d is increased as the length of the hallux and other digits, W increases as the *cube* of linear body-dimensions. Thus, the hallux needs to be long relative to general body dimensions. In ground-walking and running, on the other hand, a long, abducted hallux and long digits would be of little value, and probably in fact a positive handicap.

It is quite clear that the Olorgesailie *Simopithecus* most closely resembled the highly terrestrial gelada in those characters of the foot which are good indicators of

FIG. 31. Forces acting upon a foot gripping a horizontal branch with the hallux, when the animal's weight-line is displaced beyond the branch. (Modified after Gray, 1943).

arboreal/terrestrial adaptation. Bearing in mind that larger monkeys need relatively longer halluces than smaller ones of the same degree of arboreal adaptation, it is particularly striking that a *Theropithecus oswaldi mariae* male, an animal perhaps the size and weight of a female gorilla, had a hallux no larger than that of a mandrill, a semi-arboreal animal weighing only about one-third as much, and could not have obtained a foothold on branches more than about 3 inches in diameter. The implication is that it could not have climbed trees or walked along branches as part of its daily routine, and probably could do so only in a clumsy manner in an emergency or for a night-refuge. Of course, the short, stout digits and weak hallux would be no handicap to an animal which climbed crags or rock-faces, as does the living gelada, and it is possible that *Simopithecus* was also dependent upon such places for night-refuges. In this case, however, its environmental requirements (both permanent, fresh water and crags within its daily range) would be more demanding than is indicated by its wide range and common occurrence in fossil faunas. Alternatively, it is possible that the larger *Simopithecus* roosted on the ground, relying on their strength as a defence against predators, in the same way as living male gorillas.

The Olduvai II *Simopithecus* evidently had digits that were as short and stout and a hallux as reduced, as those of its descendants at Olorgesailie (Fig. 15), a clear indication that it, too was a ground-living animal. The evidence of the humeri, with rather large and projecting brachioradialis flanges and stout ulnar epicondyles, seems rather to indicate an animal with powerful elbow and digital flexors, and hence a semi-arboreal way of life. There are two possible explanations for this apparent inconsistency; either the humeri belonged to another large cercopithecoid, not *Theropithecus*, or else the *Simopithecus* line was still in process of adaptation to full terrestrial life during the early Middle Pleistocene, and, having acquired the short digits of a ground-living monkey, had yet to lose the large flexors of a semi-terrestrial form.

We have no information about the postcranial skeleton of the remaining *Simopithecus* forms.

C. Adaptations to diet in the Dental and Cranial Anatomy of *Simopithecus*

In section V we determined the trends in dental and gnathic evolution which distinguish *Theropithecus* from other large Papionini. It is possible to interpret these characteristics as a single, diet-related functional complex. Observations of living animals indicate that the dentition of Cercopithecoidea may be considered in terms of three functional regions: incisors, cheek-teeth, and canines + P_3. The *incisors* are mainly used in the preliminary processing of food-objects as these are held in the hand, more specifically for separating the edible portion from the inedible, which is then discarded. Tasks in this category include biting through the husks of fruits, nibbling the flesh of fruits from the rind, and, occasionally, the meat of mammals or birds from the skin or bones, and stripping or plucking buds, leaves or small fruits from a stem or branch as it is drawn between the teeth. Quite often, especially in the case of leaf-eating Colobinae (Ripley, 1970) the branch is not broken off before being brought to the mouth for stripping, and occasionally the incisors are used to prise a closely adherent food-object from an immovable substrate. They are however, not used in a manner analogous to the grazing of ungulates, to pluck small, easily picked food objects from the ground or other fixed substrate; such objects are invariably picked up by hand, or, occasionally, with the lips or tongue. The small incisors characteristic of *Theropithecus* suggests that such preparatory activities are a relatively unimportant part of its feeding habits, and thus that its diet includes a relatively minor proportion of items requiring preparation before mastication. This is consistent with the known diet of *T. gelada*, which consists very largely of small objects which are gathered by hand and placed in the mouth whole. The diet of *Papio*, on the other hand, especially in the overlap zone, includes a high proportion of items, largely tree-products, requiring such preliminary preparation (Crook and Aldrich-Blake, 1968), and the rapid wear to which the incisors, though large, are subject, is attested by wild-shot skulls.

The *premolars and molars* (apart from P_3) are concerned with trituration of the food mass after preliminary preparation, if any. The movements involved have yet to be fully elucidated by cineradiography, but appear to be mainly lateral (Mills, 1963). In *Theropithecus*, the amount of occlusal surface available for this function is very large, relative to body-weight as compared to, for instance, *Papio*. For example, in a sample of nine males of *Papio ursinus ursinus* (Jolly, 1965) the mean 'area' of the upper cheek teeth (sum of length × breadth) is 568 cm^2; in the *T.* (*S.*) *oswaldi oswaldi* male, an animal of closely comparable bulk, it is 868 cm^2. This feature indicates a diet in which the major food items are tough and therefore require extensive chewing to break them down, or low in nutritional value per unit volume, so that large quantities must be processed. Both these attributes apply to the predominant foods of *T. gelada*, which has been observed to spend a greater proportion of its time than other baboons in feeding (Crook and Aldrich-Blake, 1968).

In all Cercopithecoidea, the molars and premolars show high relief in their crowns, as compared to Hominoidea, among which only the gorilla approaches the condition normal in the monkeys. In Colobines and *Theropithecus* however, occlusal relief is further exaggerated in association with a diet which (like that of *Gorilla*) includes a high proportion of the vascular parts of plants. In Colobinae, the major cusps are linked by high cross-lophs, and there is a tendency to reduce structures mesial and distal to the principal cusp-pairs. The effective surface is therefore made up of a series of sharp transverse ridges, upper interlocking with lower, a pattern which persists until an advanced stage of wear, and is presumably related functionally to chopping foliage. In the molars of *Theropithecus*, extreme crown height and relief is associated with *additional* clefts and fossae, especially mesial and distal to the major cusps, with the formation of a prominent *longitudinal* ridge, and with a wear pattern in which the occlusal surface of the molar crown is reduced to a plane surface at an early stage. Clearly a different adaptive pattern is involved, in which the grinding surface is provided by the pattern of enamel ridges, the remains of the walls of the cusps and the inter-cusp crests, which project from exposed dentine in the worn tooth-surface. When wear is advanced, the only relief is provided by 'studs' of enamel which originally formed the floor of the deepest inter-cusp hollows.

With these gone, the molar must be considered virtually useless for grinding, having only a continuous dentine surface.

The adaptive advantage of the *Theropithecus* molar over the bunodont *Papio* type is first that, the greater complexity of invaginations provides more enamel ridges on the surface of a worn tooth; second, that the more parallel-sided and deeper inter-cusp clefts and basins prolong the presence of these enamel ridges to a more advanced stage of wear, and third, that the high crowns provide more material to be abraded and thus postpone dental obsolescence still further. This functional pattern accords well with the graminivorous diet of *T. gelada*; grasses, by virtue of their siliceous cell-coats are resistant to digestion, and thus require fine trituration before swallowing to release their nutrients. For the same reason, and because of the soil particles which are likely to be ingested with them, they are extremely abrasive.

The hypothesis that this type of molar is adaptive to a diet consisting largely of grasses is supported by the fact that cheek teeth with high crowns, more complex ridging, and columnar shape accompany grazing habits in mammals as diverse as Perissodactyls (Equidae), ruminant Artiodactyls (Bovidae etc.), Suidae (*Phacochoerus* and allied forms), Proboscidea (Elephantidae) and Rodentia (Microtinae).

As noted previously there is some evidence that in the subgenus *Simopithecus*, at least, the third molars tended to come fully into occlusion late, relative to the first molars and to the anterior teeth, especially the male canine. It is impossible to tell, from fossil material, whether this represents merely a modification of eruption within a period of dental development that was no longer in total than the cercopithecoid norm, or whether the third molars erupted later in the life of the animal. Whether relative or absolute, however, the delayed eruption of M_3 would seem to represent an adaptation combating heavy molar wear, by replacing and crowding forward worn-out anterior molars, while retaining the mechanically advantageous short dental row. This would not be possible if all three molars were present and in occlusion in their unworn condition. Again, there is a parallel to grass-eating mammals of other orders, notably horses and elephants.

The *canines* of Cercopithecoidea (together with the anterior face of P_3, which functionally belongs with them) are used in fighting rather than feeding. The tendency towards reduction of canine height in males, characteristic of subgenus *Simopithecus*, was, however, probably dietary in origin. As in other Anthropoidea apart from Hominidae, the occlusal plane in worn molars and premolars of *Theropithecus* is inclined buccally, the lingual cusps of the upper teeth, and the buccal cusps of the lower, sustaining the heavier wear. This asymmetry is clearly related to the projecting crown of the upper canine which limits horizontal movement during the lingual phase of chewing by coming into contact with the 'honing' face of P_3. In female Cercopithecinae, the canine tip not infrequently wears to the level of the crowns of the other teeth, and a flatter wear-plane is produced in the post-canine region. In males, however, except in rare individuals, the canines, although they may become worn and often broken, continue to project, maintaining asymmetrical wear on the cheek-teeth, throughout life. In these cases, final obsolescence of the individual cheek-tooth occurs with the breakdown of the enamel wall of the more severely worn side, lingual in the upper teeth, buccal in the lower. In *Thero-*

pithecus with its back-tooth dominance and abrasive diet, prolongation of the life of the molars and premolars was clearly at a special evolutionary premium, and two adaptations appear to have arisen to meet the challenges of canine-induced asymmetrical wear. First, the additional height added to the tooth-crown as hypsodonty evolved was allocated more heavily to the side of the crown subject to the heavier wear in life. The resulting asymmetrical hypsodonty, with crowns higher on the lingual side in the upper teeth, and the buccal in the lower, is characteristic of both subgenera of *Theropithecus*. The second adaptive trend seen clearly only in *Simopithecus* was to reduce the height of the male canine. This probably had little effect upon molar wear during its early stages, but would raise the probability of the canine's wearing flat before the collapse of the molars, thus prolonging their life (and that of the animal), by allowing a period of symmetrical wear. The predictable end-point of such a trend would be a condition like that in early Hominidae, where the canine crown projects so little when unworn that it invariably wears to the level of neighbouring teeth, and permits symmetrical molar wear, from an early stage.

Again, this hypothesis finds some support in the fact that modifications of the canine, with the effect of permitting horizontal occlusion and free lateral movement of the cheek-teeth, are practically universal in mammalian groups adapting to grazing or to other ways of life dominated by heavy chewing. Grazing pigs (*Phacochoerus* and its allies) retain but re-orient the upper canines so that they do not interlock; the various groups of pecoran and perissodactyl grazers greatly reduce or eliminate them. Among primates, reduced canine crown height is evident in the three other genera which most clearly exhibit signs of adaptation to heavy chewing: the hominoids *Gigantopithecus* and *Australopithecus* and the lemuroid *Hadropithecus* (Simons and Ettel, 1970; Jolly 1970a, 1970b).

In those groups in which canine modification has taken the form of reduction rather than re-orientation, the evolutionary problem has arisen of developing alternative means of combat and defence, and has been variously solved by the elaboration of somatic or extra-somatic weapons (antlers, horns, artefacts). Unfortunately when *Simopithecus* became extinct, its canines, though much reduced from the cercopithecoid norm, were still large and projecting enough to preclude the need for such alternative weapons.

The cranial indications of massively-developed muscles of mastication, especially pterygoids and masseter, seen in *Theropithecus* are again consistent with a diet requiring heavy molar and premolar chewing. The narrow postorbital constriction, anterior position of the union of the temporal lines and vertical orientation of the ascending mandibular ramus all attest to a temporal muscle the mass of which is more anteriorly placed than that of *Papio* or *Mandrillus*, and whose fibres are more nearly perpendicular to the occlusal plane. The deep posterior maxillae may be seen in part as a way of preserving this vertical orientation while accommodating allometric lengthening of the face. The mechanics of mastication in monkeys have yet to be analysed experimentally. However, simple geometrical relationships between the occlusal plane and the approximate resultant forces of the masticating muscles suggests a functional explanation of the *Theropithecus* pattern. Contraction of the muscle results in forces of occlusion and of retraction. The latter, when generated by bilateral contraction, are presumably involved in incisal 'nibbling', while the former, generated by alternating contraction of the musculature of either side, are synergic to the action of masseters and pterygoids in opposing the occlusal surfaces of the cheek-teeth and moving the mandible laterally in 'rotary' chewing. The orientation of the temporal in *Theropithecus*, by increasing the angle between its line of action and the occlusal plane towards 90°, increases the occlusal but decreases the retractive component of its action Analogous variation is seen in other mamalian groups. Aside from the Carnivora, forms with the mandibular condyle set on or approaching the occlusal plane are to be found chiefly among the rodents in which incisor function is clearly dominant; significantly, *Daubentonia* and the extinct 'gnawing' Prosimii (e.g. *Plesiadapis*) also show this condition. In grass-eating animals with grinding molars, on the other hand, the mandibular condyle is set well above the occlusal plane, and as far forward as is anatomically possible, producing a vertical ascending ramus. Such a condition is seen in, for instance, the grazing horses and Artiodactyls, the elephants, and the grazing pigs. In the case of the Proboscidea (Osborn, 1936–42); and the Suidae (Ewer, 1956) there is evidence of the evolution of grazing forms with high, vertical ascending rami and hypsodont cheek-teeth from bunodont ancestors with lower rami and presumably a diet of fruits and tubers. It is tempting, therefore, to consider the vertically-oriented ascending ramus of *Theropithecus*, with which may be correlated the forwardly-set temporal muscles, as similarly adaptive to a diet consisting largely of grass.

Structures in the glenoid region – the antero-posteriorly narrow glenoid fossa, confined posteriorly by a stout post-glenoid process, the mandibular condyle with its articular surface confined almost entirely to its superior aspect – can also be plausibly interpreted as correlates of masticatory habits in which lateral chewing movements predominate.

VII. SUMMARY AND DISCUSSION

The genus *Theropithecus* seems to be derived from a primitive, African, stock of Papionini which began to exploit the open-country grassland niche not later than the middle-to-upper Pliocene. A stock of primitive *Theropithecus* probably became isolated in the Ethiopian highlands, and gave rise to the modern gelada, while the other forms continued to specialize in the lowlands. Like their living relative, the latter were inhabitants of open country, rarely if ever climbing trees, and preferred the margins of shallow lakes where seasonal flooding inhibited the growth of trees but enriched the ground-flora, especially of grasses. Blades, seeds and rhizomes of grass, picked by hand, probably supplied the bulk of the diet, but would have been supplemented by other small food-objects.

The extinction of subgenus *Simopithecus* which seems to have occurred about 50,000 years ago, requires no explanation in terms of widespread climatic change. As in the case of other large, comparatively slow-moving animals, the influence of human hunters is likely to have been a highly significant factor in the disappearance of the genus from most of its Pleistocene range. As has been emphasized elsewhere, higher primates are peculiarly vulnerable to over-hunting because of their slow reproductive rate (Jolly, 1966), which makes them dependent for survival upon a high rate of success in rearing young to maturity. The larger forms of *Simopithecus* are likely to have been even more slow-breeding than their smaller contemporary relatives. The disappearance of *Simopithecus* corresponds to a wide-ranging impoverishment of the African mammalian fauna, mainly by the extinction of larger forms (Cooke, 1963), and, significantly, to a period of diversification of human cultures and elaboration of hunting techniques (Clark, 1959, Cole, 1954). At both Olduvai and Olorgesailie there is evidence of extensive hunting; at the latter site *Simopithecus* was apparently a staple food during one period of human occupation (Isaac, 1966).

On the other hand, it would be naive to suppose that *Simopithecus* was literally exterminated by the hand of man. Rather we should see human interference as disturbing an ecological balance between it and related genera, especially *Papio*. Of the two, *Simopithecus*, slower moving, less able to escape by climbing, larger, but less well-equipped with canine teeth, probably slower breeding, and dependent upon long daily periods of uninterrupted feeding in the very lakeside habitat which was apparently the favoured hunting and gathering ground for early man, was much the more likely to be adversely affected by human predation, competition and simple disturbance. Each reverse to *Simopithecus* would have been to the advantage of sympatric populations of *Papio* baboons, whose generalized structure enables them to respond flexibly to predation and competition from humans, yet which, as their modern distribution and natural history shows, are quite capable of exploiting opportunistically those resources which primitively were the domain of *Theropithecus*, and which remain so in its refuge areas of the high Simien.

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PLATE 1

Skulls of extant Cercopithecinae

a. ***Mandrillus leucophaeus***, male × ½
b. ***M. leucophaeus***, female × ½
c. ***Theropithecus gelada***, male × ½
d. ***T. gelada***, female × ½

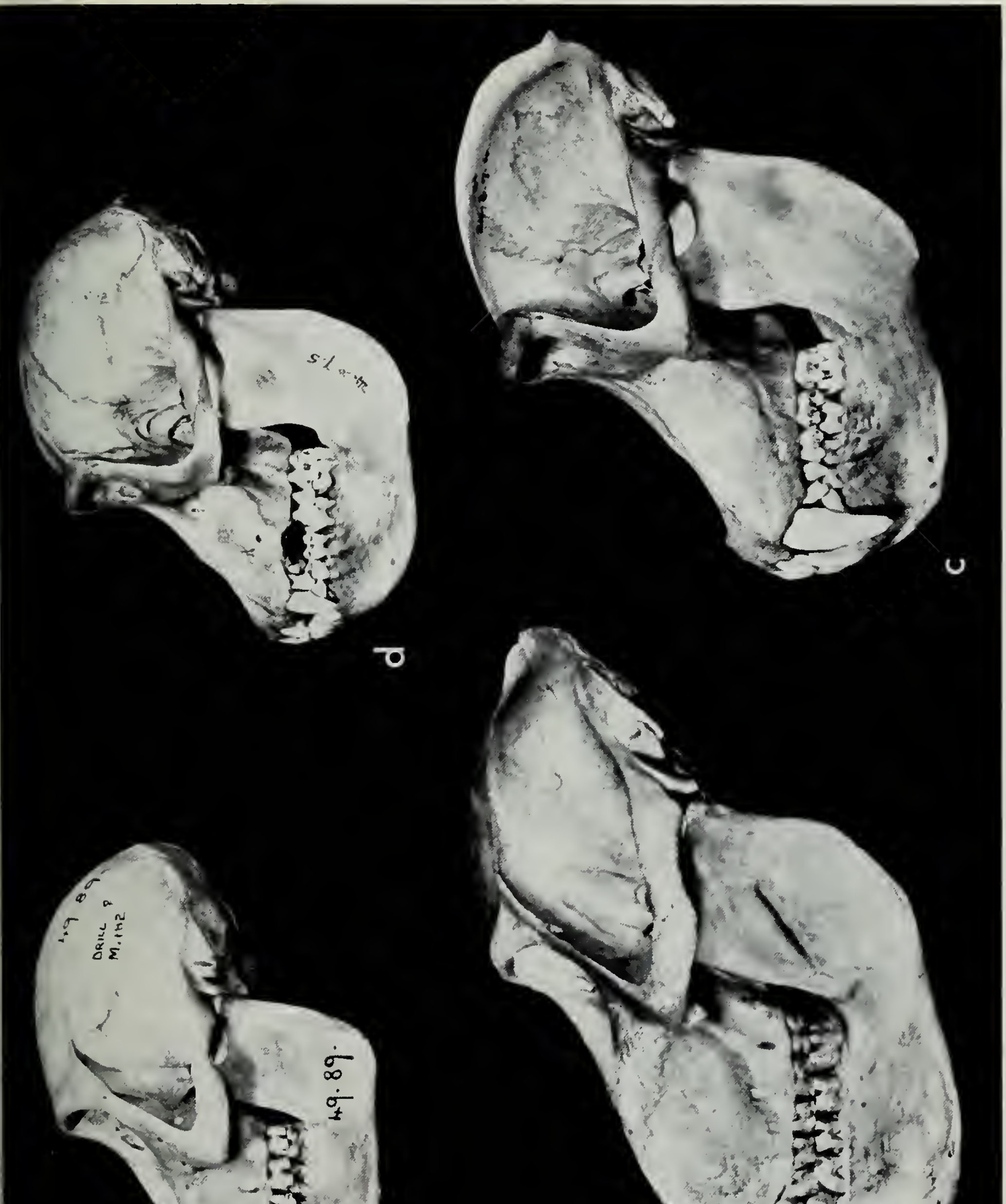
a
b
c
d

PLATE 2

a. ***Papio cynocephalus kindae***, male × ½
b. ***P. c. kindae***, female × ½
c. ***Papio ursinus***, male × ½
d. ***Papio ursinus***, female × ½

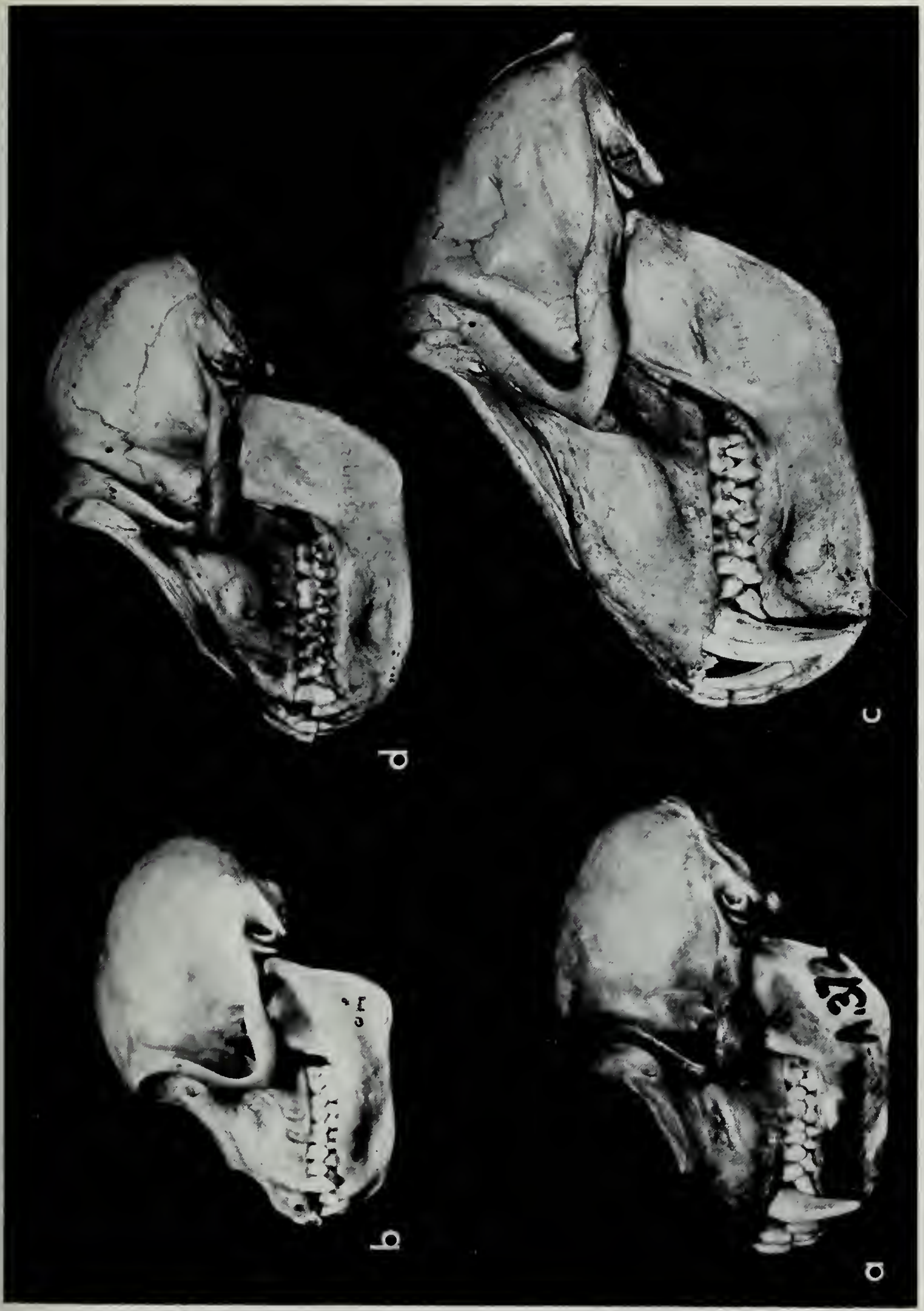
a
b
c
d

PLATE 3

Theropithecus oswaldi oswaldi

a. Male cranium, F 3668	× $\frac{1}{2}$
b. Female P_3, M 18763	× 2
c. Male P_3, M 18755	× 2
d. Female lower canine, M 18753	× 2
e. Male lower canine, M 18729	× 2

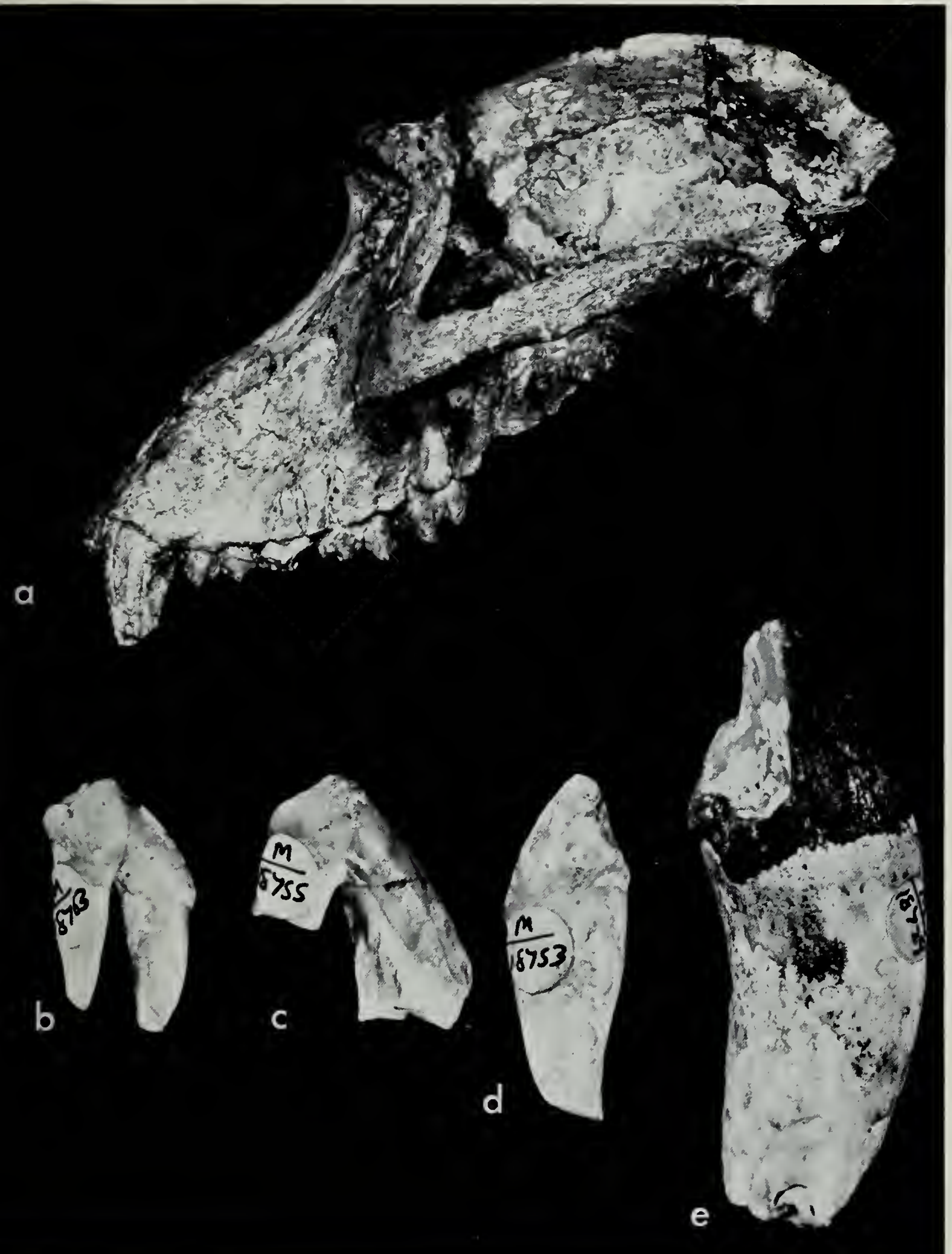
a
b
/8763
c
M
18755
d
M
18753
e

PLATE 4

Theropithecus oswaldi oswaldi

a. Male cranium, F 3668	× 2/3
b. Frontal, M 18765	× 1
c. Frontal, F 3394	× 1

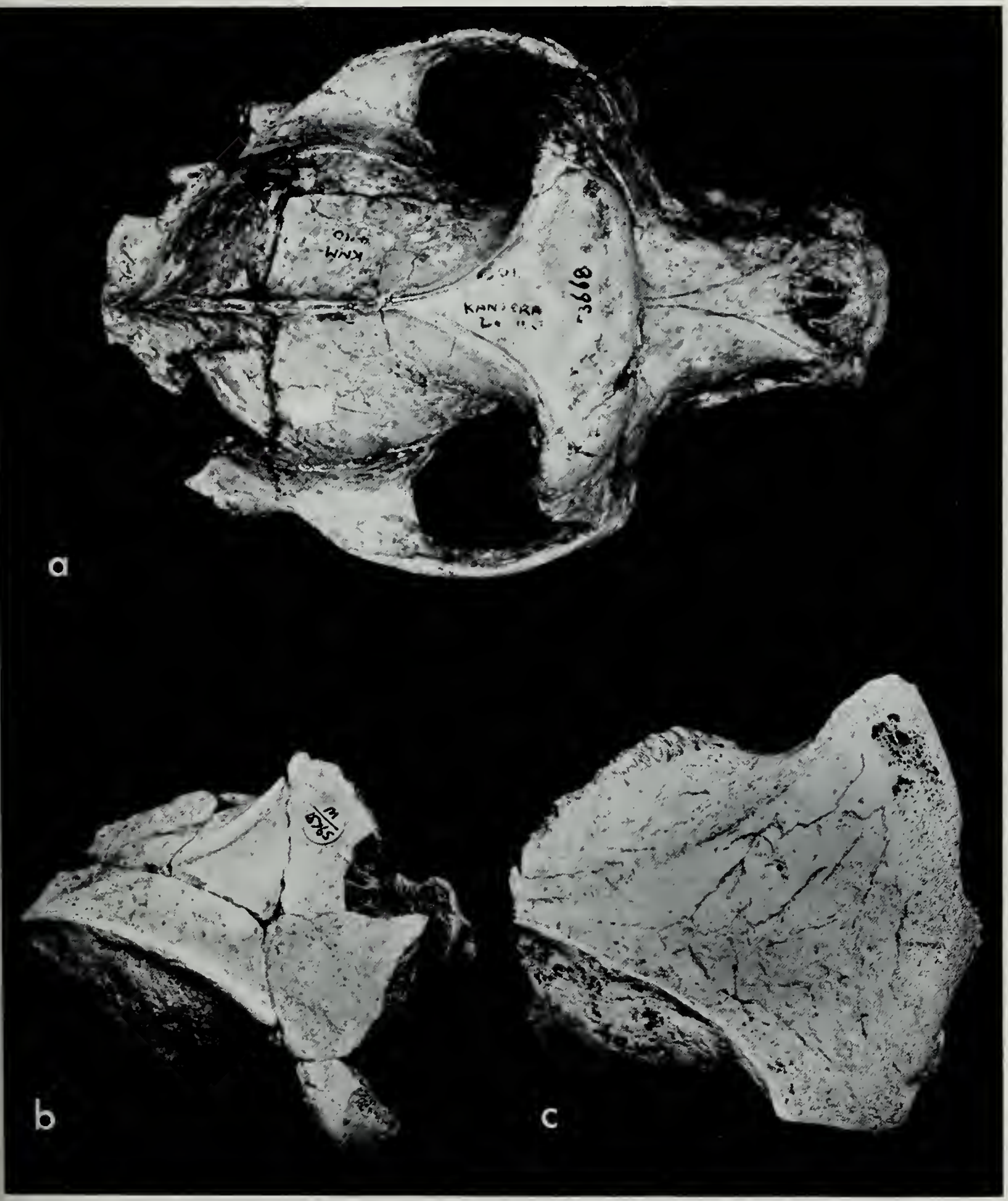
KNM
KANJERA
3668
a
b
c

PLATE 5

Theropithecus oswaldi oswaldi

a, b. Female cranium, M 14936 × 2/3


a
b

PLATE 6

Theropithecus oswaldi oswaldi Female

a. Cranium, M 14936	× 2/3
b. Maxillary dentition, M 14936	× 1
c. Anterior muzzle, M 18720	× 1
d. Cranium, M 14936	× 2/3

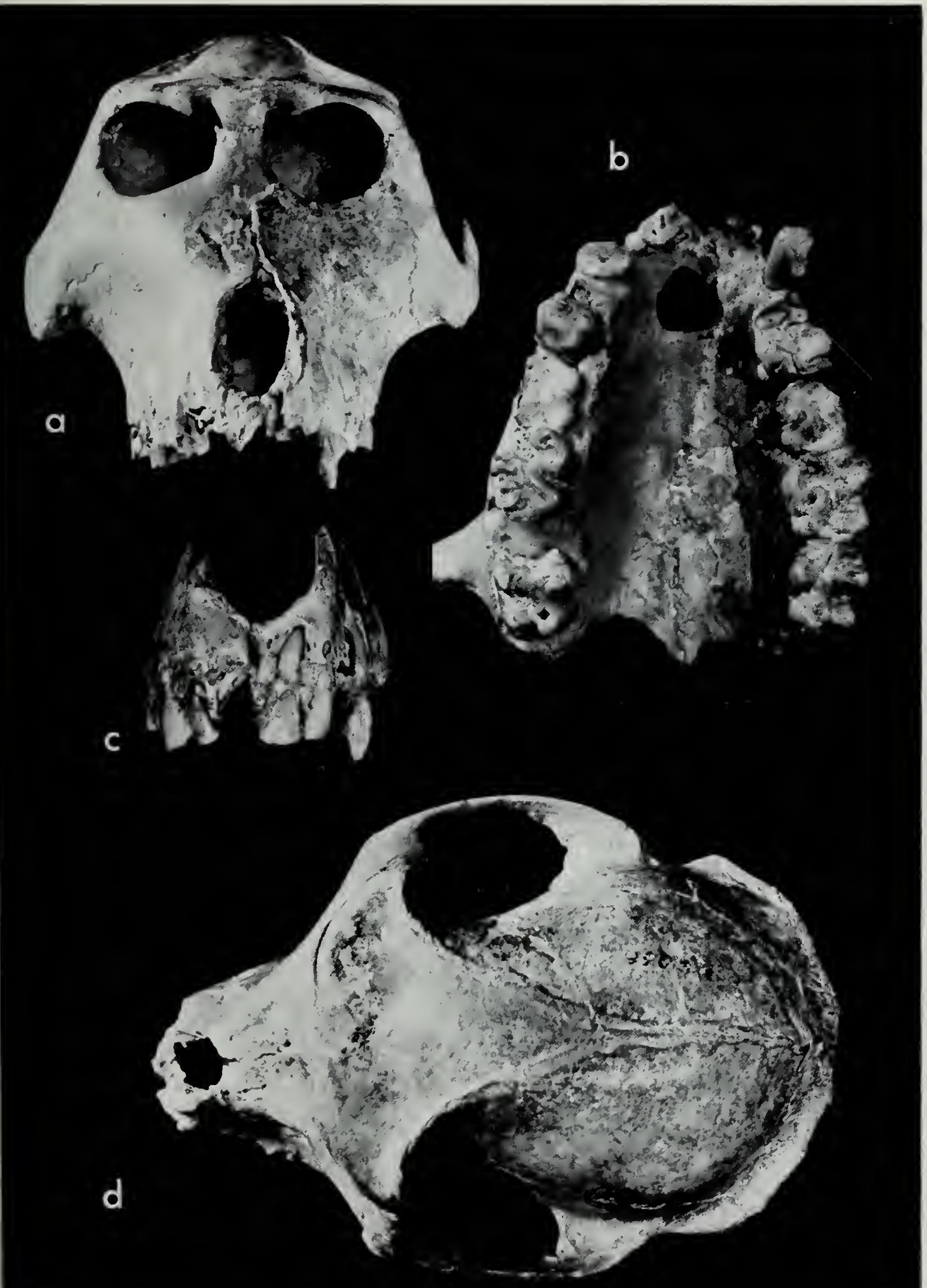
b
a
c
d

PLATE 7

Theropithecus oswaldi oswaldi Female

a. Reconstructed muzzle, M 11538 and M 18720	× 1
b. Maxillary dentition, M 11538 and M 18720	× 1
c. Muzzle, M 11537	× 1
d. Maxillary dentition, M 11537	× 1

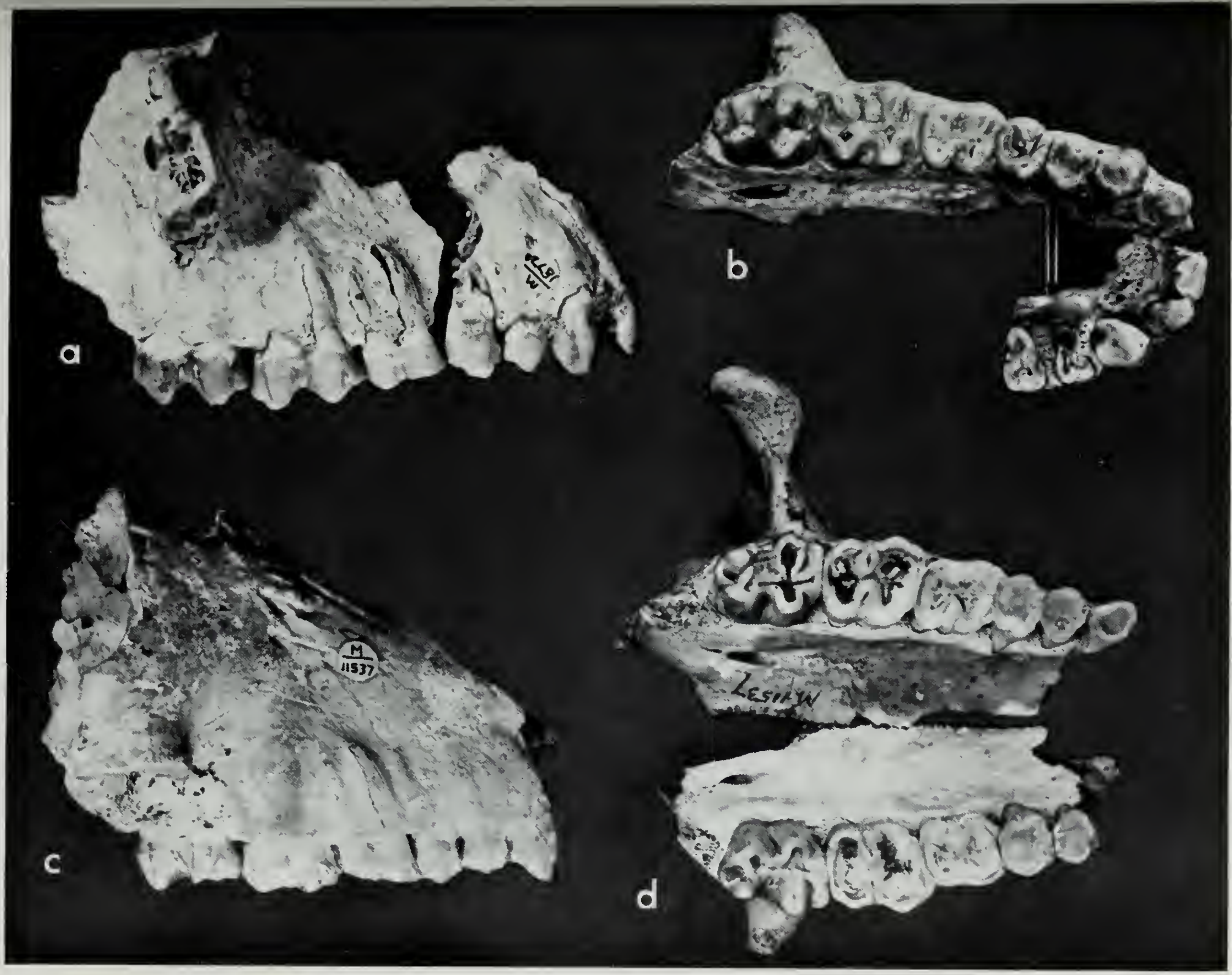
a
b
c
d
M
11537

PLATE 8

Theropithecus oswaldi oswaldi

a, b. Cranial fragment, M 18764	× 1
c, d. Female mandibular fragment, M 19011	× 1

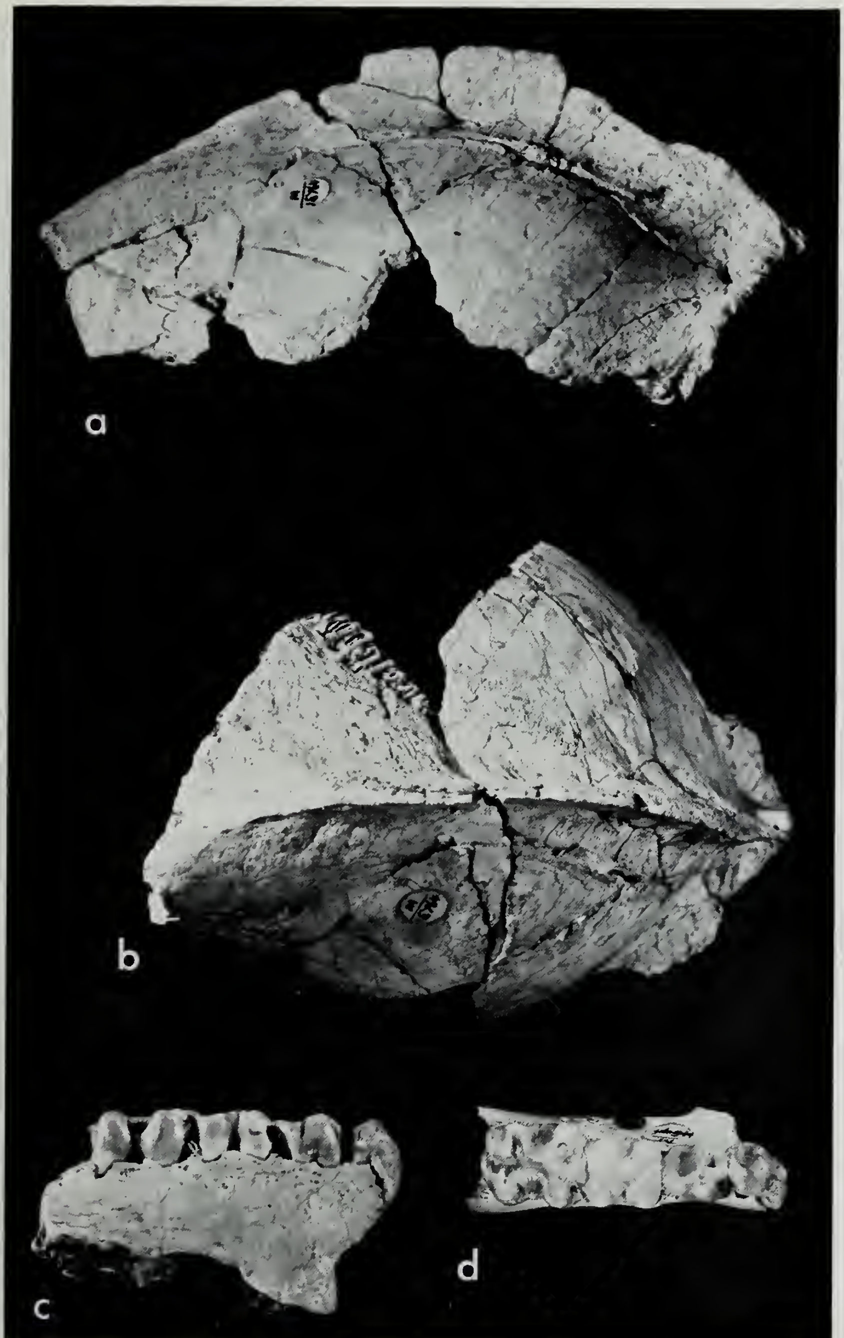
a
b
c
d

PLATE 9

Theropithecus oswaldi oswaldi

a. Mandibular fragment, probably male, M 11541	× 1
b. Female mandible, M 11539 (Type of *Simopithecus oswaldi*)	× 1
c. Juvenile female mandible, F 3398	× 1
d. M_3, light to moderate wear	× 2
e. M_3, light wear	× 2


a
M 11541
d
b
M 11539
e
c
KJ. SURF.
22.XII.21
F3378

PLATE 10

Theropithecus oswaldi oswaldi

Mandibular dentitions,

a. M 11539 (Type of *S. oswaldi*)	× 1
b. F 3398	× 1
c. M 11541	× 1


a
c
b

PLATE 11

Theropithecus oswaldi oswaldi

a, b. Scapular fragment (no. 3 in list)	× 1
c. Humeral fragment, anterior aspect, M 18789	× 1
d. Humeral fragment, anterior aspect, M 18721	× 1
e. Humeral fragment, anterior aspect, M 11542	× 1


a
b
c
d
e
KT.
M
18787

PLATE 12

Theropithecus oswaldi oswaldi

a-c. Ulnar fragments, radial aspect	
a. M 11546	× 3/4
b. M 18723	× 1
c. M 18726	× 1
d. M 18801 Radial fragment, probably male	× 1
e. M 11544 Radius, probably female	× 1

PLATE 12

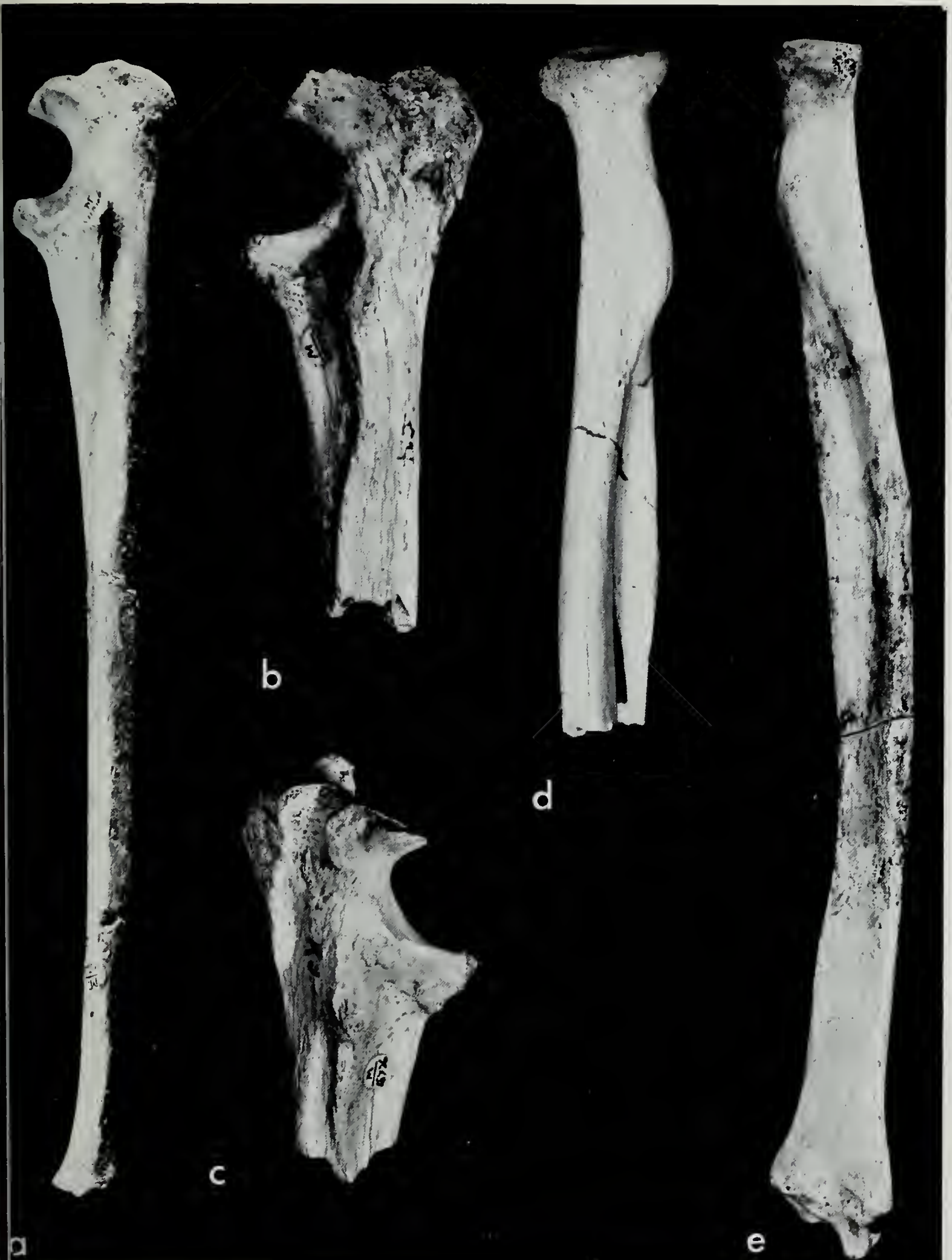

PLATE 13

Theropithecus oswaldi oswaldi

a. Femoral fragment, M 11548	× 1
b. Femoral fragment, M 18708	× 1
c. Femoral fragment, M 18707	× 1
d-f. Associated talus, M 11549, calcaneus, M 18806 and cuboid, M 18805	× 1


a
b
c
d
e
f

PLATE 14

Theropithecus oswaldi subsp.

a. Frontal fragment, M 18772 × 1
b, c. Maxillary fragment, M 14681 × 1
d, e. Maxillary fragment, M 18779 × 1

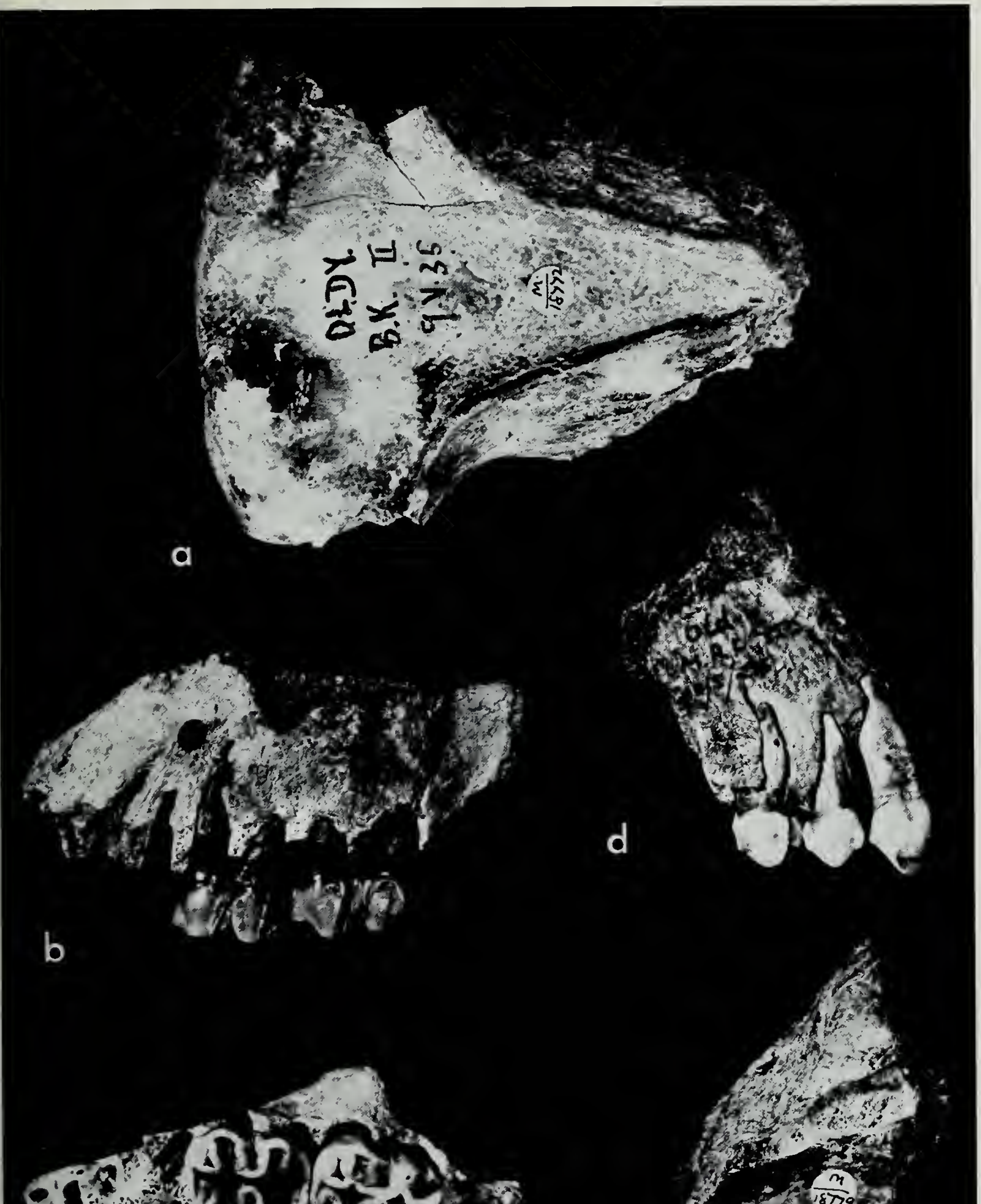
a
b
c
d
e

PLATE 15

Theropithecus oswaldi subsp., Olduvai

a,b.	Juvenile female mandibular fragment (c in list)	× 1
c,d.	Female mandibular fragment, M 14953	× 1


a
c
b
d
M.14953
M
14953

PLATE 16

Theropithecus oswaldi leakeyi and ***Theropithecus darti,*** Olduvai

a, b.	Juvenile male mandibular fragment (Type of *Simopithecus leakeyi*) M 14680	× 1
c, d.	*Theropithecus darti* (Lower Bed II). Female mandibular fragment, M 14938	× 1

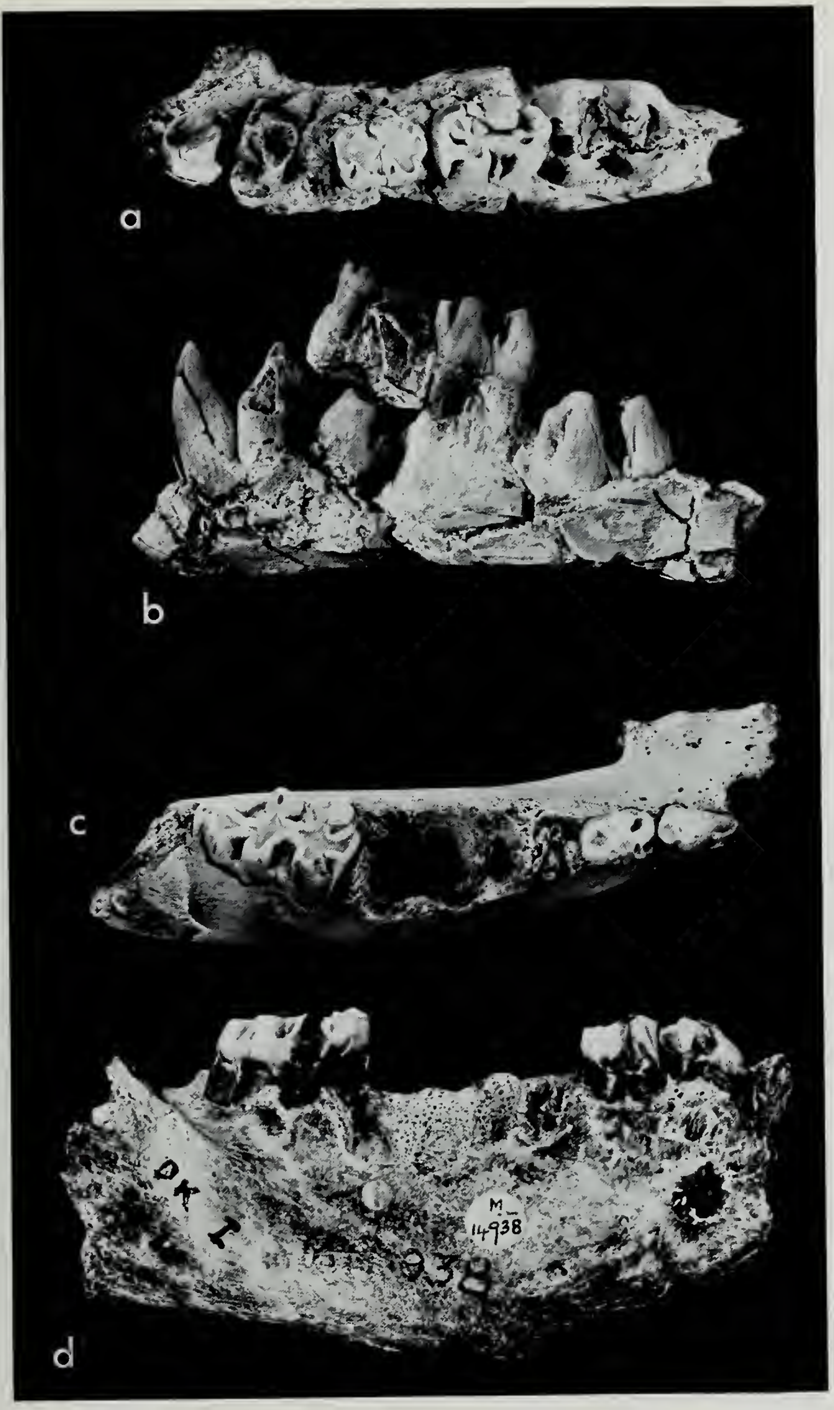
a
b
c
d
DK I
M
14938

PLATE 17

Theropithecus oswaldi subsp., Olduvai

a. Female calvarium (b in list)	× 2/3
b. Femoral fragment	× 2/3
c. Humeral fragment	× 2/3
d. Humeral fragment	× 2/3

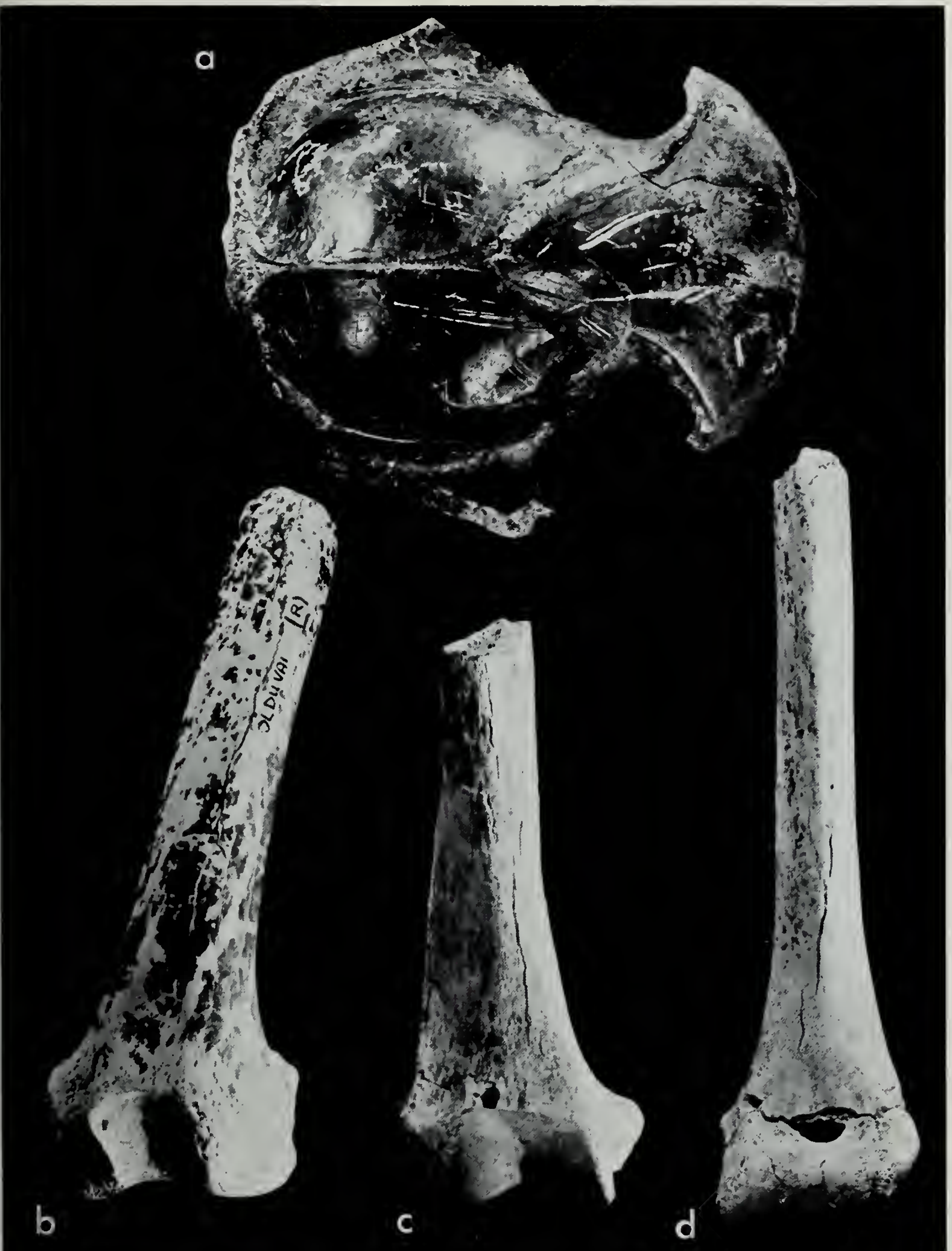
a
OLDUVAI
(R)
b
c
d

PLATE 18

Theropithecus oswaldi mariae, mandibular fragments

a. Female KNM-OG 0002 (Type)	× 1
b. Juvenile male KNM-OG	× 1
c. Juvenile male KNM-OG	× 1

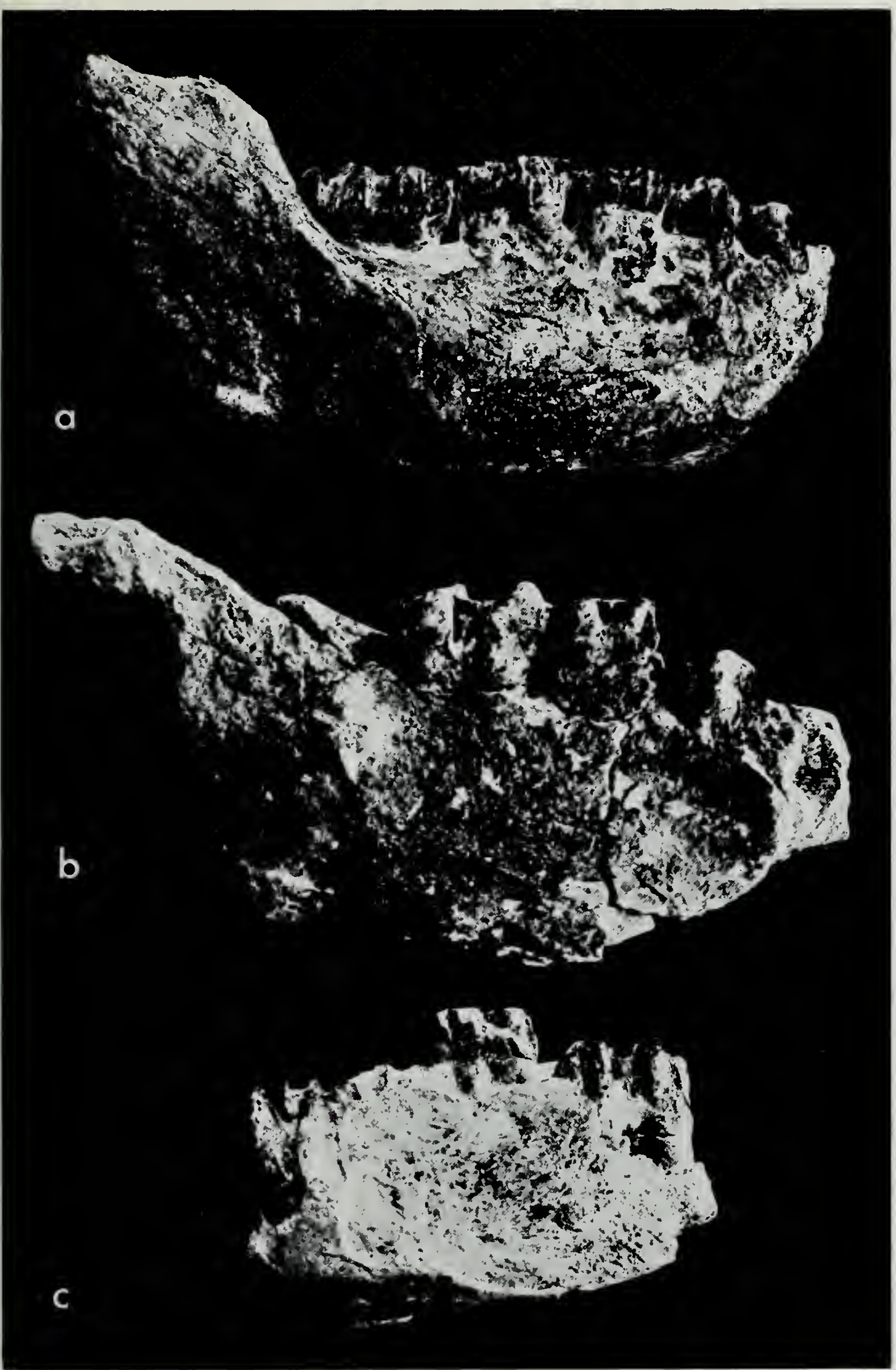
a
b
c

PLATE 19

Theropithecus oswaldi mariae

a,b. Adult male KNM OG-4	× 1
c. Adult male KNM OG-5	× 1
d. Juvenile maxillary fragment KNM OG-1	× 1

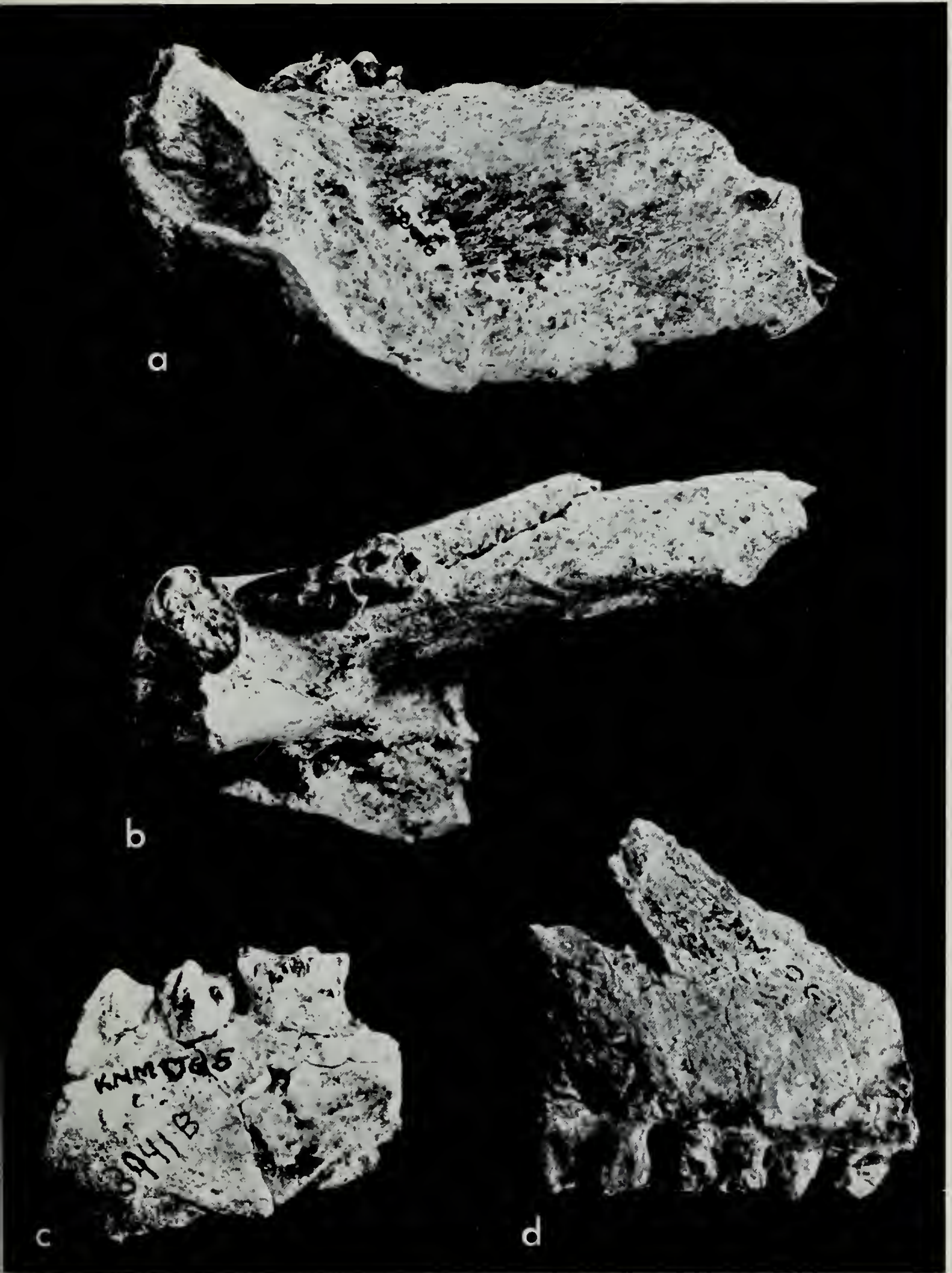
a
b
c
d

PLATE 20

Theropithecus oswaldi mariae

a. Humeral fragment, KNM-OG 1056. Probably subadult male × $\frac{1}{2}$
b. Femur, KNM-OG 10990. Probably female. × $\frac{1}{2}$
c. Femoral fragment, KNM-OG 1088. Probably male × $\frac{1}{2}$


a
b
c